SOME ASPECTS OF THE BIOLOGY OF

ANTHOXANTHUM ODORATUM L.

A Thesis presented for the
degree of Doctor of Philosophy in Botany
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by

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FOREWORD

Sweet vernal grass, Anthoxanthum odoratum, is a European grass introduced into New Zealand by the white settlers. It has become established over a very extensive part of the country. It has a very wide ecological amplitude and is found mostly on low fertility soils, in both wet and dry environments; it is common where the original vegetation has been disturbed. It occurs in particular in poor or neglected pastures, along roadsides and in the high country of New Zealand. This is the country lying above the arbitrarily chosen line of 200 m. above sea level. Since this area is very extensive and of considerable economic importance, it has been suggested (for example by the Tussock Grassland Research Committee, 1954) that the grasses common in that environment should be studied. A. odoratum was chosen because of its wide distribution, its early spring growth and its use as an indicator plant for nutrient availability in different soils.

LAY-OUT AND ABBREVIATIONS

The thesis is divided into Chapters and Sections by using a numerical system.

Tables are numbered according to the Section to which they refer followed by letters in lower case, in alphabetical order, e.g. Table 5.7.a.

Figures are also numbered according to the Section to which they refer followed by capital letters in alphabetical order, e.g. Figure 5.7.A.

Fertilizers are abbreviated according to the chemical symbols of their main components; e.g. N, P, K, Ca for nitrogen, phosphorus, potassium and calcium.

Wind-directions are abbreviated as N, W, S, E (north, west, south and east).

Temperature is expressed as degrees Centigrade unless otherwise defined.

Metric weights and measurements are used throughout.

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ABSTRACT

Several aspects of the biology of Anthoxanthum odoratum have been studied in this thesis. The results are based on evidence obtained from the literature and on findings from experiments carried out by the candidate. This thesis has been arranged to give a balanced picture of the biology of sweet vernal grass without over-emphasis on the experiments carried out as it was felt that this would disjoint the lay-out. The main experiments are contained in Chapters 2, 5, 6 and 7.

Since A. odoratum is a very polymorphic grass, plants have been collected from five localities in New Zealand (Kaikohe, Te Awa, Lincoln, Gore, and Porter's Pass) to reduce bias in the experimental results. Although this grass has been in New Zealand for about one hundred years only, physiological and morphological differences were found to occur among the plants from these localities. These findings may reduce the significance of the results obtained with A. odoratum as an indicator plant for nutrient availability in different soils. Therefore, it has been recommended in Chapter 6 to use only those A. odoratum plants with known-fertility response pattern for nutrient availability studies. In Chapter 10, the importance of this ecotypic differentiation, its evolutionary significance and its use for plant breeders has been discussed. Only incipient ecotypy could be recognized and no new taxa have been described.

RESUME OF CHAPTERS

Chapter 1. Taxonomy and Evolution

From a review of the taxonomy, evolution and distribution of the genus Anthoxanthum it has been concluded

that this genus is closely related to the genus Hierochloë; similarities and differences are outlined.

It has been postulated that the widespread genus Anthoxanthum is a very old one in which the basic chromosome number, x has been reduced from 7 to 5. A map of its natural distribution has been drawn and a subdivision into three groups has been suggested.

From a review of the morphology and evolution of the species A. odoratum, it has been concluded that this outbreeder is a very polymorphic and adaptable grass.

Borrill and Jones have suggested that A. odoratum is an allotetraploid, probably derived from the hybrid A. alpinum x ovatum.

Chapter 2. Life History

The life history of A. odoratum has been reviewed and supplemented by experiments on seed weight, germination percentage, requirements for floral induction, panicle emergence, seed production, seed longevity and by a description of seedling development. It has been found that:

1. the 1000 grain weights of New Zealand seeds are less than those of European samples;
2. the germination percentage of New Zealand seed samples approximates that of European samples;
3. there is a definite low temperature requirement to obtain the reproductive phase; at high temperatures, short-day treatment had some, but long-day treatment had no effect on the attainment of competence for inflorescence development. Among the plants from the five localities, those from northern sites had a lower low temperature requirement than those from southern sites;

4. panicle emergence is influenced by both temperature and daylength. When grown in an experimental garden, the panicles from plants from northern sites tended to emerge earlier than those from plants from southern sites;

5. one plant may produce 30,000 or more viable seeds;

6. the viability of seed stored in a laboratory for three years is nearly identical to that of fresh seed;

7. seedling development appears to be rapid; as long as sufficient moisture and warmth is available, seedlings can grow under extremely low fertility conditions;

8. it is concluded that A. odoratum is an extremely efficient colonizer.

Chapter 3. Agricultural Importance and Introduction into New Zealand

The agricultural importance of A. odoratum has decreased from a pasture grass in the early days of settlement to the present status of a "weed", but it may increase again if low coumarin, high producing strains can be bred.

Investigations have shown that A. odoratum was present in New Zealand in 1847, which is the earliest documented record available so far.

The rapid spread of A. odoratum has been illustrated in a table and it has been found that in 1862 it occurred as far inland as Lake Pukaki, but not as far as Mt Cook as reported by Hooker.

Chapter 4. Ecology

The ecological range of A. odoratum in Europe and New Zealand has been reviewed and it has been concluded that sweet vernal grass occurs up to a certain altitude above sea level wherever the native vegetation has been disturbed in New Zealand.

The reasons for the ecological adaptability of A. odoratum have been based on findings presented in Chapters 1 and 2.

The agricultural ecology has been reviewed and it was found that A. odoratum:

1. is low yielding in comparison to improved pasture grasses;
2. responds to nitrogenous but also to phosphatic fertilizers;
3. survives better under hard grazing than under lax grazing;
4. is grazed to some extent in autumn, winter and spring.

Chapter 5. Plant and Environment

The performance of A. odoratum under several types of pasture management was reviewed in Chapter 4. To explain this performance, three experiments were designed.

In the first experiment, the vegetative growth of A. odoratum plants from five localities in New Zealand under autumn and spring conditions combined with sunny and shady treatments was investigated. It was found that:

1. Physiologically different behaviour occurs among the A. odoratum plants from these five localities. The Kaikohe locality contains winteractive plants, whereas the Porter's Pass locality contains winter-dormant plants.
2. Winteractive behaviour in the Kaikohe (and sometimes in the Te Awa) plants was observed in:
   (a) Relative increase of total plant dry weight.
   (b) Growth rate of leaf blade length.
   (c) Tiller formation of fourth and fifth degree tillers.

(d) Growth rate of total interblade length.

3. Winterdormant behaviour in the Porter's Pass plants was observed in:

   (a) Relative increase of total plant dry weight.

   (b) Length of third leaf.

   (c) Growth rate of leaf blade length.

   (d) Daily tiller increment.

   (e) Tiller formation of fourth and fifth degree tillers.

   (f) Growth rate of total interblade length.

4. The plants from the remaining localities, Lincoln and Gore, fitted in between these extremes.

5. The Lincoln plants produced fewer tillers but larger leaves so that the total plant dry weight was still comparable to that of the others.

6. A. odoratum behaves like other festucoid grasses with respect to rootgrowth, tiller production and rate of leaf appearance although its productivity is low.

In the second experiment, the behaviour of A. odoratum when competing with two other low fertility grasses, Agrostis tenuis and Holcus lanatus for N, P and S fertilizers and space was investigated. It was found that:

1. its tiller production is not affected by the two associate grasses, Agrostis tenuis and Holcus lanatus over a period of three months;

2. its herbage production is reduced by A. tenuis and even more so by H. lanatus; under the "high cut" treatment the effect is more pronounced than under the "low cut";

3. its tiller and its herbage production is affected in approximately the same manner by fertilizers, mainly N : first N depression, then N response; its response to P is low; S depressed tiller number under "high cut" treatment, tended to do so under "low cut" and did not affect herbage production.

In the third experiment, the colonizing potential of A. odoratum when growing near its altitudinal limit was investigated. It was found that:

1. Vegetative vigour is low even after applying N and P fertilizers. It is adversely affected by grazing, short growing season, spring drought, and strong drying winds. Without fertilizers establishment is very difficult on low fertility soils.

2. It needs two months of relatively frost-free weather to produce flowers and to set seed. Frosts shrivel up panicles.

3. For establishment its "seeds" need cover to provide moisture and to prevent frost heave.

4. It does not produce sufficient mulch in which other plants can become established. Its mulch disintegrates readily under the influence of wind, frost, snow, rain and limited microbiological activity.

Chapter 6. Indicator Plant Experiment

A. odoratum has been used as an indicator plant for the nutrient availability in different soils in New Zealand. However, in Chapters 2 and 5, physiological differences were found among the plants from five localities. Since this could affect the significance of the results obtained with A. odoratum as an indicator plant, an experiment was

designed to assess the fertility response pattern of cloned plants raised from seed from these five localities and grown in two different soils.

It was found that A. odoratum plants from a montane locality take up decisively different amounts of P and S (but not of K) when compared to plants from four lowland localities.

It was therefore recommended that only plants with known fertility response pattern should be used for the testing of nutrient availability in soils by means of indicator plants.

Chapter 7. Morphological Differences

Since A. odoratum is a polymorphic grass and since physiological differences had been found among plants from five localities, it was decided to measure both direct transplants and plants grown from seed from these five localities in an experimental garden. From the measurements on culm length, panicle length and culm number, it was found that:

1. Although A. odoratum has been in New Zealand now for about one hundred years, it is still a highly variable plant from a morphological point of view.

2. Transplants are rapidly modified by experimental garden conditions, especially with regards to culm number and panicle length.

3. Plants from seed may be even more rapidly modified by experimental garden conditions.

4. The morphological differences observed in the Lincoln group of plants tend to become genetically fixed.

5. The montane Porter's Pass plants are more adaptable than all other plants studied.

Chapter 8. Coumarin

The sweet smell of A. odoratum is due to coumarin. A review of the literature revealed that it has many physiological effects both on animals and plants. The coumarin concentration in A. odoratum is not high enough to cause sweet clover disease in grazing animals. Coumarin, normally a germination inhibitor, increases germination of A. odoratum seeds. Coumarin is rapidly broken down in moist soils by microbiological activity, but in dry soils it may have some effect on plants.

Chapter 9. Diseases and Insect Attacks

In spite of the presence of coumarin, which is an antifungal substance, A. odoratum is attacked not only by fungi, but also by viruses and insects. A brief list of pathogens has been compiled from the literature, supplemented by unpublished identifications.

Chapter 10. Discussion and Conclusion

The physiological and morphological differences found among A. odoratum plants from five localities in New Zealand have been interpreted as incipient ecotypy, so that no new taxa have been described. The evolutionary significance of ecotypic differentiation has been investigated and a diagram of micro-evolution has been drawn up. The use of incipient ecotypy to plant breeders has been emphasized and it is considered that sufficiently diverse material of A. odoratum is available in New Zealand to start a plant breeding programme.

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CHAPTER 1

TAXONOMY AND EVOLUTION

1.1 INTRODUCTION

The genus Anthoxanthum is usually regarded as a European genus but as is shown here it is distributed throughout the world. The natural distribution of the species A. odoratum is limited to Europe and Siberia but it has been introduced by European settlers to most temperate regions of the earth. The genus Anthoxanthum is closely related to the genus Hierochloë. Similarities and differences between these two genera are outlined. British workers have suggested that the species A. odoratum is of allopolyploid origin. Their work is summarized here as it explains the taxonomical status of A. alpinum Löve and Löve, sometimes regarded as a diploid form of A. odoratum.

1.2 TAXONOMIC STATUS OF THE GENUS

The genus Anthoxanthum was described by Linnaeus in Genera Plantarum 1737 and the species odoratum in Species Plantarum 1753. The generic name Anthoxanthum is derived from the Greek: ἄνθος = flower and ξανθός = yellow, referring to the golden colour of the panicles when they are ripe. The specific epithet odoratum is from the Latin: odoratus = flavoured, referring to its smell of coumarin, especially when drying. The common name sweet vernal grass also refers to the sweet coumarin smell, and to its earliness in spring.

The genus Anthoxanthum is classified in the tribe Phalarideae of the subfamily Festucoideae. In most

genera in this subfamily and even in this tribe the basic chromosome number (x) is 7 (Bowden, 1965), but Anthoxanthum is unusual in having x = 5. Avdulov (1931) regarded this as reduction in the basic chromosome number and attached considerable evolutionary significance to it. Anthoxanthum may be regarded as an aneuploid genus in the Festucoideae, because of its unusual basic chromosome number.

Other genera in the tribe Phalarideae are Phalaris and Hierochloë. The close affinity of the genus Hierochloë to Anthoxanthum is shown by these various interpretations:

1. Ohwi (1947) transferred four species from Hierochloë to Anthoxanthum.

2. Hierochloë horsfieldii (Kunth) Maxim. and Anthoxanthum horsfieldii (Kunth) Mez are both based on Ataxia horsfieldii Kunth.

3. Anthoxanthum japonicum (Maxim.) Hack. has 2n = 70 (Tateoka, 1954). It may be 14 x, based on x = 5, or a decaploid, based on x = 7. If the basic chromosome number is 5, then this species is closer to Anthoxanthum but if x = 7, then it may be closer to Hierochloë.

The chief morphological distinctions between the two genera Anthoxanthum and Hierochloë are:

(1) Usually both lower florets in a spikelet are neuter in Anthoxanthum but staminate in Hierochloë. (In A. siamense (Bor, 1963) one lower floret is staminate.) Incorrect observation of this fact by Hitchcock led to confusion in the case of A. angustum (Reeder, 1950; Jansen, 1953).

(2) The glumes are of unequal length in Anthoxanthum (the lower glume is shorter than the upper one), but are of equal length in Hierochloë.

(3) Anthoxanthum very rarely forms rhizomes, whereas Hierochloë does (Jansen, l.c.).

(4) Lodicules are absent in Anthoxanthum but are present in Hierochloë.

(5) Most Anthoxanthum species have hairy auricles, but Hierochloë species hardly ever have them.

(6) Anthoxanthum usually has only two stamens whereas Hierochloë has three.

No evidence of transfer of species between the genera Anthoxanthum and Phalaris has been found, and therefore the differences between these two genera have not been outlined.

To obtain a better delimitation of the genera Anthoxanthum and Hierochloë, detailed karyological studies to support morphological evidence will have to be carried out. Whether chromosome counts provide a simple means of separating Hierochloë with x = 7 from Anthoxanthum with x = 5 is not clear, as there are Anthoxanthum species with 2n = 70, e.g. A. japonicum. This species may be 14x, based on x = 5, or a decaploid, based on x = 7. It seems likely that the genus Anthoxanthum has undergone a reduction in basic chromosome number from x = 7 to x = 5. No evidence could be found which explained how this reduction might have taken place in Anthoxanthum, although Darlington (1963) has outlined how changes in the chromosome complement may occur in plants. He also discussed B-chromosomes which are frequently found in the genus Anthoxanthum (Östergren, 1942, 1947; Hedberg, 1952, 1957; Rozmus, 1963; Jones, 1964).

B-chromosomes are small, accessory chromosomes which do not pair with ordinary chromosomes at meiosis, but only with one another. They vary in number among different individuals and can sometimes be entirely dispensed with. The B-chromosomes must also be derived chromosomes: derived recently or ultimately from the ordinary or A-chromosomes (Darlington, l.c.). Östergren (1947) found that the B-chromosomes of Anthoxanthum have the ability to maintain themselves in populations although they are not homologous with ordinary chromosomes. The centromeres of these B-chromosomes are but little defective and show surprisingly good pairing with one another at meiosis. Up to four B-chromosomes have been found in the genus Anthoxanthum. It is tempting to suggest that they are remnants of the 6th and 7th chromosome of the ancestor of Anthoxanthum, but this is merely conjecture.

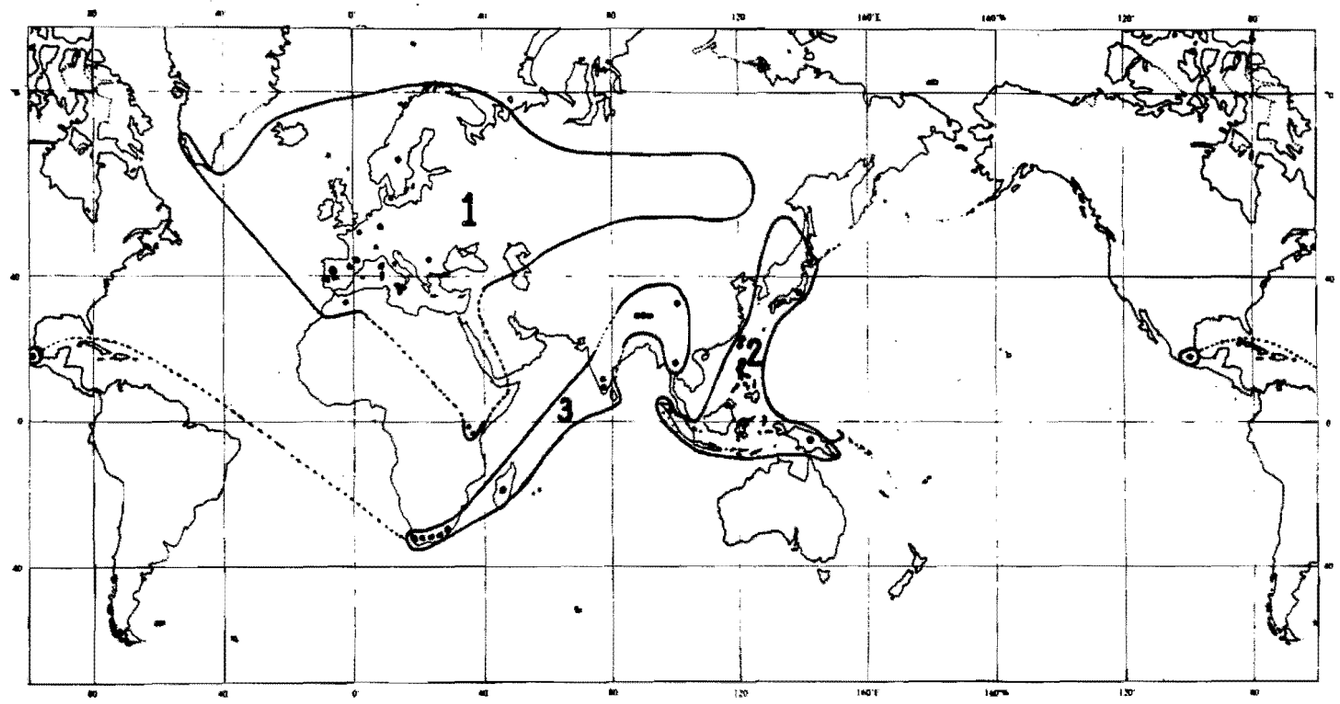
Hovin and Hill (1966) state that "Several workers have concluded that the accessory or B-chromosomes of gramineous species have a very ancient origin (Östergren, 1947; Müntzing, 1954; Nygren, 1957). For instance, Müntzing suggested that the occurrence of B-chromosomes in rye was a primitive trait and was important in determining the centre of origin of cultivated rye". These statements may also apply to the genus Anthoxanthum. Therefore, I would like to postulate that this genus is a very ancient one, but one that is still very vigorous as shown by the extremely variable species A. odoratum and the A. nivale-A. scaposum complex in Africa, described by Hedberg (1952, 1957).

1.3 DISTRIBUTION OF THE GENUS

It is usually considered that the genus Anthoxanthum occurs only in Europe including Iceland and Greenland,

around the Mediterranean, on Mt Kilimanjaro in Africa, in the Caucasus, Russia, and Northern Asia, but three species have been described from Japan, and others have been found in the Philippines, Formosa, Malaya, Sumatra, Java, Borneo and New Guinea (Chase, 1962), Thailand (Bor, 1963), India, Madagascar and South Africa. Except for one species in Mexico, none have been recorded in the Americas, Australia and New Zealand, apart from introduced species, although Dichelachne crinita Hook.f. had as its basis A. crinitum Linn.f. One of these Far Eastern species A. luzoniense Merr. is reported to be very similar to A. odoratum (Jansen, 1953), but so far no chromosome counts on A. luzoniense and hybridizations between A. luzoniense and A. odoratum have been carried out. Another species, A. nipponicum var. furumii Honda has since been renamed A. odoratum var. furumii (Honda) Ohwi. Recent work of Tateoka (1966) on A. nipponicum Honda shows that this species may be conspecific with A. alpinum Löve and Löve, which in turn is morphologically very hard to distinguish from A. odoratum. A. nipponicum occurs in alpine belts of the Akaishi Mountain Range, Rishiri Is., Mt Hotai in Korea and in Manchuria. A. alpinum is found in Greenland, Iceland, Scandinavia, the European Alps, Carpathian Mountains, Transsylvanian Alps and the northern parts of Central and Western Siberia (Tateoka l.c.). This example of close affinity between a European and an Asian species of Anthoxanthum, helps to bridge the gap between the geographically widely separated groups of species of this genus. At some future date, the morphologically similar species A. luzoniense and A. odoratum may be shown to be conspecific too.

The widely distributed species of Anthoxanthum may be divided into three groups as shown in Figure 1.3.A:



DISTRIBUTION OF THE GENUS *ANTHOXANTHUM* AND SUGGESTED SUB-DIVISION INTO GROUPS.

EACH DOT REPRESENTS A SPECIES

Figure 1.3.A Natural distribution of the genus Anthoxanthum and suggested subdivision into groups.

(1) The European-North African group with hybrid populations and species of wide ecological amplitude. Stapf called this the section Eu-Anthoxanthum (Thiselton-Dyer's Flora Capensis, Gramineae VII, p.466). The group comprises species occurring in Europe, including Greenland, Iceland and the U.S.S.R.; the Mediterranean including North Africa as far south as Mt Kilimanjaro and other areas studied by Hedberg (1952, 1957). To this group belong: A. aertnense Lojac., A. alpinum L. & L., A. amarum Brot., A. angustifolium Plan., A. aristatum Boiss., A. asperum Mann ex Opiz, A. carrenianum Parl., A. gracile Bivon., A. laxiflorum Bubani, A. lloydii Jord. ex Boreau, A. myrthense Lojac., A. nebrodense Lojac., A. nivale K. Schum., A. odoratum L., A. ovatum Lag., A. pauciflorum Adam., A. puelii Lec. et Lam., A. scaposum Peter.

(2) The Far East group with no hybrid populations and species of very limited ecological amplitude. Most species are restricted to isolated mountain peaks in the tropics and subtropics. The group covers Japan, Formosa, the Philippines, Malaya, Sumatra, Java, Borneo and New Guinea. To this group belong: A. angustum (Hitchc.) Ohwi, A. formosanum Honda, A. horsfieldii (Kunth) Mez, A. japonicum (Maxim.) Hack., A. khasianum (C.B. Clarke) Ohwi, A. luzoniense Merr., A. neesii Mez, A. nipponicum Honda, A. papuanum P. Jansen, A. sumatranum P. Jansen, A. viridescens Honda.

(3) The Ataxia group (formerly the genus Ataxia) and some allied species. This group covers Mexico, South Africa, Madagascar, India, Burma, Thailand and China.

To this group belong: A. avenaceum Retz., A. brevifolium Stapf, A. clarkei (Hook.f.) Ohwi, A. dregeanum (Nees) Stapf, A.gracillimum (Hook.f.) Mez, A. hookeri (Griseb.) Rendle, A. madagascariense Stapf, A. mexicanum (Rupr.) Mez, A. pallidum (Hand.-Mazz.) Kong, A. siamense Bor, A. sikkimense (Maxim.) Ohwi, A. tenue (Trin.) Mez, A. tongo (Trin.) Stapf.

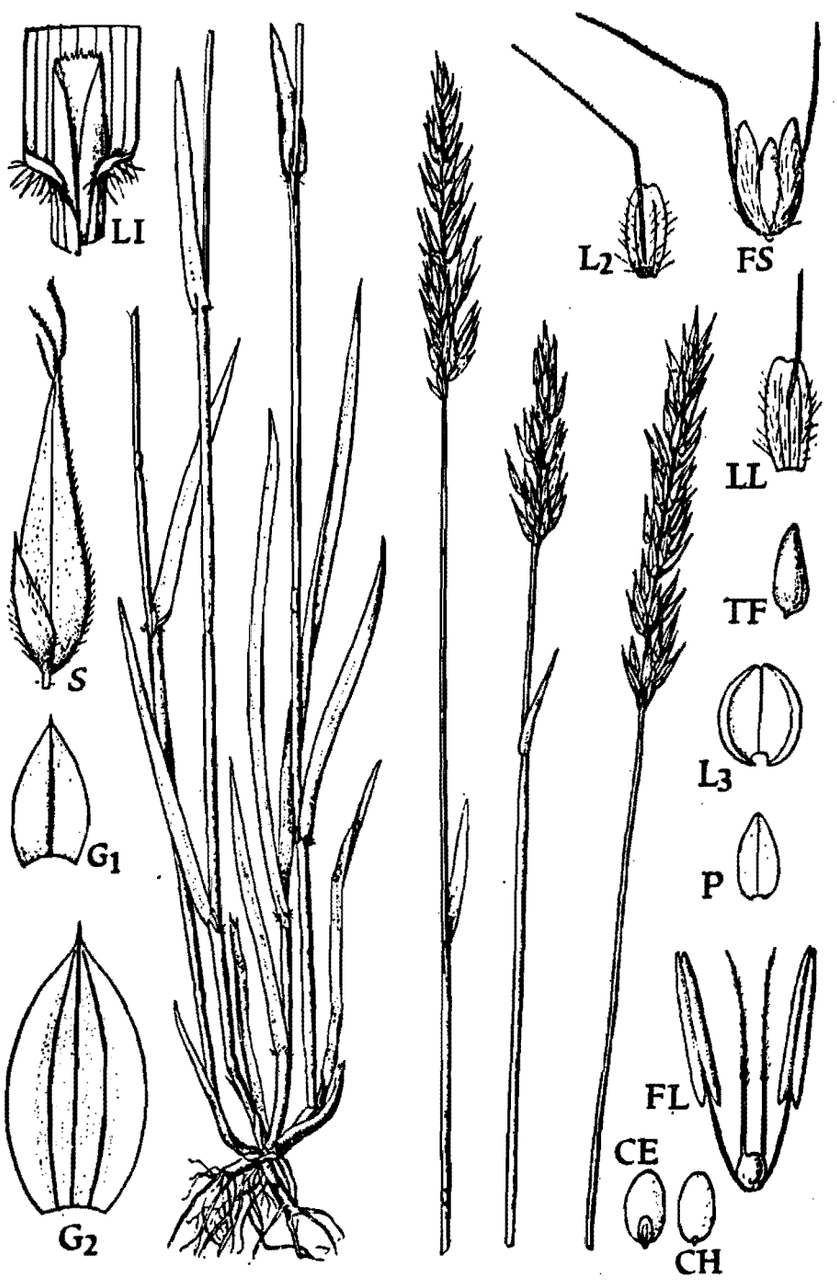
The above list of species has been compiled from Chase (1962) except for A. siamense Bor.

Groups (1) and (2) tend to merge as shown by Tateoka (l.c.) for A. alpinum and A. nipponicum and by Ohwi (1965) for A. odoratum and A. odoratum var. furumii. It is possible that groups (2) and (3) are linked by A. sumatranum and A. siamense, and groups (1) and (3) by Central and South African Anthoxanthum species, but these links have not yet been suggested in the literature.

The distinctness of these three groups may be highly debatable, but it may illustrate that a taxonomic revision of the genus Anthoxanthum is long overdue and it may lead to some very interesting discoveries, including a sharper definition of this genus and the genus Hierochloë.

1.4 MORPHOLOGY OF THE SPECIES

A recent description of the species A. odoratum can be found in Hubbard (1954). Figure 1.4.A shows that this perennial grass forms an erect, tufted plant with unbranched, 1-3 noded culms, 10-100 cm high. Panicles are spike-like and rather dense, 1-12 cm long, 6-15 mm wide. Spikelets (S in Figure 1.4.A) consist of three florets (FS), the lower two barren, the third (TF) bisexual, the three falling together at maturity. Glumes are persistent, the lower glume (G_1) about half the length of the upper (G_2). Sterile lemmas (LL and



Anthoxanthum odoratum. Very common; grassland.

Figure 1.4.A Anthoxanthum odoratum (from C.E. Hubbard, 1954, p.244).

L_2) are brown and hairy, the lower (LL) with a straight awn and the upper (L_2) with a bent awn (for detail see Figure 2.10.A). Fertile lemma (L_3) and palea (P) tightly enclose the grain (CE, CH). Flower (FL) with only 2 anthers. Leaf-blades are finely pointed, 1-12 (up to 30) cm long and 2-5 (up to 10) mm wide; blade-base densely hairy. Ligule (LI) finely serrate, 1-5 mm long, white, often purplish.

The species A. odoratum is strongly protogynous and therefore an outbreeder. For this reason it is extremely variable and adaptable to many habitats. It is a vast source for those taxonomists who want to describe varieties, subvarieties and forms. In Chase (1962) some 50 varieties, 8 subvarieties and 13 forms are listed. Many of these appear to be extremely debatable but without the type specimens and extensive collections in the type localities, no further work can be done.

Strelkova (1932) who made a detailed study of A. odoratum stressed that the stability of various taxonomic features can only be determined from "rather lengthy experiments" and she found that two seasons of observations on transplants in a nursery were too short to make a full analysis and evaluation of distinct forms. She criticized Kolokolnikov's taxonomic study of A. odoratum because he appeared to have used herbarium material only. Earlier studies on A. odoratum by Rozanova (1926) had also shown that the variability of a taxonomic character was affected differently by different environmental factors and that the effects set in earlier for some characters than for others.

Recent work of Sharman (1960a, b) on the development of the spikelet of Anthoxanthum showed that there is only one primordium and not three, so that only one flower, the fertile one is formed. He claims that the lower

two barren florets commonly recognized by most taxonomists in the spikelet of Anthoxanthum, do not exist. Earlier work by Rozanova (1925) lead Avdulov (l.c.) to conclude that the flower of A. odoratum is extremely reduced morphologically but very advanced from an evolutionary point of view. A. odoratum also has a very low chromosome number (Section 1.2), which in Avdulov's opinion further supports the idea that there is a general tendency to reduction of the basic chromosome number in the Gramineae.

I have not seen any rhizomatous A. odoratum plants in New Zealand although Strelkova (1932) found such plants in Russia (see Sections 2.5 and 2.12). The Portuguese species, A. amarum Brot. has swollen buds (bulbils), which do not simulate rhizomes. The buds give rise to young tillers, but they probably serve as storage organs which may aid the development of these tillers in autumn after the hot Mediterranean summer, during which root growth is likely to stop.

From field observations on A. odoratum plants, it was noticed that hairiness of the leaves can vary in one population from perfectly glabrous except for the hairy auricles to a hairiness, comparable to that of Holcus lanatus. Seeds from France, labelled A. odoratum var. villosum Lois. produced plants which varied as much in hairiness as is usually found among ordinary sweet vernal populations. Therefore, I agree with Hedberg (1964) that pubescence of leaves and to some extent of glumes (which are thought to have evolved from leaves (Bowden, 1965), is a spurious taxonomic character in A. odoratum but this has already been observed by Strelkova (1932).

The monstrosity compositum, in which more than one panicle is formed on one culm, was seen occasionally in about three plants per 200. A specimen is present in the Botany Division, D.S.I.R., Herbarium, No.68802.

A specimen of the monstrosity viviparum can also be found in this Herbarium, No.121931. The word viviparum may suggest that vivipary occurs in A. odoratum but this is incorrect: only vegetative proliferations of the glumes are found and such spikelets cannot reproduce vegetatively. Domin (1941) mentions A. odoratum with white streaks in its leaves, which have been called forma pictum or picta. From field observations, I suggest that these plants were attacked by yellow dwarf virus or a related virus, and certainly not worth description as a form. Nodes of culms will only rarely form roots. It was observed once in moist glasshouse conditions at low light levels (see Figure 2.5.A).

1.5 ORIGIN AND EVOLUTION OF THE SPECIES

The evolution of A. odoratum has been studied by Borrill (1963) and K. Jones (1964). Until their work was published, A. alpinum L. & L. was usually regarded as the diploid which gave rise to A. odoratum by autopolyploidy (Tutin, 1950; Knaben, 1950; Östergren, 1942; Parthasarathy, 1939). Kattermann (1931), according to Knaben (1950), having studied meiosis, was of the opinion that structural hybridity, besides autopolyploidy accounts for the formation of multivalents in A. odoratum. Morphologically, it is hard to distinguish A. alpinum from A. odoratum (Hedberg, 1961) and the description of an A. alpinum with 2n = 20, occurring in the British Isles, only adds to the confusion (Jones, 1963). It appears that Jones (l.c.) was not very familiar with the conflicting views held by taxonomists on the status of A. alpinum, prior to the publication of the work of Borrill (l.c.) and of K. Jones (l.c.). Davis and Heywood (1963, p.220) speak of A. odoratum

and A. alpinum as cytodemes, being cytologically different but morphologically very similar. However, Rozmus (1960) has shown that anatomical differences exist between the two species, and Borrill (l.c.) and K. Jones (l.c.) have shown that A. odoratum is not an autopolyploid from A. alpinum.

The hybridization experiments carried out by Borrill (l.c.) showed that the artificial allotetraploid based on the sterile hybrid between A. alpinum and A. ovatum Lag. simulates A. odoratum more closely than do polyploids of either of the diploids. The results from these experiments also showed that the alpine perennial A. alpinum was genetically more isolated from A. odoratum than the Mediterranean annual A. ovatum. Borrill (l.c.) thinks that it is very likely that this hybridization may have occurred under natural conditions, giving rise to A. odoratum. As far as I know, he has not yet produced crosses between A. odoratum and this artificial allotetraploid. If these two plants can be crossed, analyses of the karyotypes may give further support to Borrill's supposition.

The breeding work of Borrill (l.c.) was followed up by cytological studies by K. Jones (l.c.) who was struck by the remarkable interplant variation of the karyotype morphology, which is caused by continuous repatterning of the chromosome sets. This itself argues for the fact that A. odoratum has originated from diploids whose chromosome sets differed in morphology, recombination between which could result in a range of new chromosome types. After careful comparison of the karyotypes and the meiotic behaviour of A. odoratum and its possible ancestors, K. Jones (l.c.) comes to the same conclusion as Borrill (l.c.) did: A. odoratum is of allotetraploid origin. The phenotypic polymorphism

of A. odoratum can be explained by assuming that structural rearrangements of the chromosomes during meiosis are confined to terminal segments which suggests itself by the terminal localization of the chiasmata. Pericentric regions would thus remain intact and if these regions contain the loci which determine the essential species characteristics, their controlled and balanced segregation would ensure the basic constancy of A. odoratum, whilst at the same time extensive recombination of terminal segments could produce wide variation in more peripheral characters, e.g. hairiness. K. Jones (l.c.) shows that although quadrivalent and even higher multivalent pairing is very common in Anthoxanthum a system which ensures balanced separation of the ancestral sets, can operate. In this system there is the opportunity for a degree of chromosomal and genetic recombination, which in giving rise to greater variability, can be of decided advantage to the morphologically very variable and ecologically very adaptable species A. odoratum.

1.6 SUMMARY

(1) The genus Anthoxanthum was first described by Linnaeus in 1737.

(2) The species A. odoratum was first described by Linnaeus in 1753.

(3) The morphological distinctions between the closely related genera Anthoxanthum and Hierochloë are outlined.

(4) The genus Anthoxanthum is very widely distributed throughout the world, but does not occur naturally in the Americas, Australia and New Zealand. A subdivision into three groups is suggested and the

need for a taxonomical revision of the genus is stressed. It is also suggested that the genus Anthoxanthum is a very old one from an evolutionary point of view.

(5) The species A. odoratum is an outbreeder and therefore extremely variable, both morphologically and ecologically.

(6) The evolution of the species A. odoratum is outlined on the basis of the work of Borrill and Jones, who show that this species is not derived by autopolyploidy from A. alpinum but most probably by allopolyploidy from the hybrid A. alpinum x A. ovatum.

(7) The karyological studies of Jones help to explain the wide morphological and ecological variability found in A. odoratum. He showed that in spite of quadrivalent and even higher multivalent pairing, balanced separation of the ancestral sets can occur, and that the basic constancy of A. odoratum can be maintained.

CHAPTER 2

LIFE HISTORY

2.1 INTRODUCTION

A detailed description of the life history of A. odoratum is necessary to understand the ecology of this grass, and its importance in agriculture. Various aspects of the life history have been discussed by agricultural botanists but it became evident that little work had been done on seedling development, requirements for floral induction, panicle emergence and seed setting of A. odoratum. Investigations have now been carried out on these topics and the results help to complete the understanding of the life history of sweet vernal grass.

2.2 SEED WEIGHT

The "seed" of A. odoratum when shed from the panicle is not a caryopsis but a spikelet, usually thought to consist of three florets, the lower two being barren and the uppermost bisexual. It comprises two sterile lemmas and a "seed". If the sterile lemmas are removed (and they can be removed simply by squeezing the spikelet between one's fingernails), the grain enclosed by the fertile lemma and the palea is obtained. It will be called the seed in this thesis.

TABLE 2.2.a 1000 grain weights in grammes of A. odoratum seeds and spikelets (New Zealand samples).

LOCALITY*	SEEDS		SPIKELETS (Seed with sterile lemmas)	
	1000 grain weight	Number of seeds used	1000 grain weight	Number of spikelets used
Kaikohe	0.4021	195	0.4640	250
Te Awa	0.4933	165	0.5300	250
Lincoln	0.3156	180	0.3884	250
Gore	0.4595 0.4149	215 700	0.6392	250
AVERAGE	0.4219		0.5054	

*These four localities have been described in detail in Appendix A.

In the literature, these 1,000 grain weights in grammes of "seed", which are probably of spikelets, were found:

TABLE 2.2.b 1,000 grain weights in grammes of A. odoratum (Overseas samples).

COUNTRY	WEIGHT	REFERENCE
England	0.598	Sinclair (1824)
England	0.567	Armstrong (1937)
Germany	0.615	Korsmo (1930)
Holland	0.625	Dr Ir. A.F. Schoorel (pers. comm.)
Central Europe	0.455 - 1.202	Kirchner, Loew, Schröter (1909)
Portugal	0.640	Lambrechtsen

It is clear that the 1,000 grain weight of New Zealand A. odoratum plants is low. The reason for this is not known. However, it may be due to different threshing techniques. The New Zealand "seeds" were not threshed and might therefore have contained a higher percentage of undeveloped caryopses.

For comparison the 1,000 grain weights of a number of pasture grasses are given (from Table 1, p.242, Armstrong, 1937):

TABLE 2.2.c 1,000 grain weights in grammes of some pasture grasses.

GRASS	WEIGHT
Lolium perenne	1.916
Festuca rubra	1.010
Dactylis glomerata	0.986
Cynosurus cristatus	0.596
Anthoxanthum odoratum	0.567
Poa pratensis	0.213
Agrostis stolonifera	0.090

These figures show that A. odoratum has a fairly light seed. The significance of this in distribution and establishment will be discussed in Section 2.10.

2.3 GERMINATION

Germination tests were carried out on seed samples from the localities discussed in detail in Appendix A.

The seeds were in most cases pretreated in water under vacuum for a few minutes to assist imbibition, and then treated with a 0.1% $HgCl_2$ solution to reduce fungal attack of the seeds, especially a black smut. They were

put on filter paper in petrie dishes and kept in a growth cabinet, where the average temperature was 23°C; the light source was 10 x 40 watt fluorescent tubes and 6 x 60 watt tungsten striplights, arranged 40 cm above the petrie dishes (the light intensity was about 850 fc.); the day-length was 12 hours.

Seed testing Station, Department of Agriculture, Palmerston North, examines sweet vernal seed 6 days and 14 days (final count) after it has been put down to germinate in light at 20 - 30°C. Light and alternating temperatures stimulate germination of sweet vernal seed (Kirchner et al., 1909). Table 3.3.a shows that the seeds were examined on or near those days. It also shows that after 14 days more seeds will germinate, especially Porter's Pass seed which germinates slowly, possibly due to a higher degree of dormancy.

There was considerable variability in germination among the replicates within each locality sample, but only a slight difference in germination among the localities. The seeds of the Porter's Pass sample were slower to germinate but they might eventually have approximated the germination percentages of the seeds from the other localities, had they been observed for a longer period. Armstrong (1937) in his Table II gives a "growth percent" of 70 - 80 for sweet vernal grass which is higher than the overall average of 65% obtained from the data presented in Table 2.3.a. Kòrsmo (1930) quoting Stebler, puts the germination percentage at 50.

The germination percentage is suppressed by the presence of a black fungus, Aspergillus sp. and thrips (Chirothrips spp.) and bacteria. They may reduce the germination very markedly. Sewell (1947) obtained germination percentages of only 6% and 8% for A. odoratum "seed" collected in montane tussock grasslands, South

Locality*	Sowing Date	No.of seeds used	Number of days after sowing									Total
			6	8	9	11	13	14	17	28		
Kaikohe	10.5.62	100	30	33		54		59				59
	"	34		29				41				41
	"	33	39		42		48	54				54
	"	100	50		53		63	67				67
	14.5.63	100	12		55		70		76	82		82
	"	112	39		63		79		85	91		91
TOTAL			170	62	213	54	260	221	161	173		394
AVERAGE			34.0	31.0	53.2	54.0	65.0	55.2	81.5	86.5		65.7
			6	8	9	11	13	14	17	28		
Te Awa	11.5.62	120	26	42		59		62				62
	"	100	35		51		71					71
	"	80	46		57		75					75
	14.5.62	100	16		34		49		55	65		65
	"	97	11		33		63		72	79		79
TOTAL			134	42	175	59	258	62	127	144		352
AVERAGE			26.8	42.0	43.7	59.0	64.5	62.0	63.5	72.0		70.4
			6	8	9	12	13	14	15	17	28	
Lincoln	12.5.62	100	15		29	33			34			34
	"	100		61		64		65				65
	14.5.62	100	18		39		55			61	65	65
	"	91	30		51		74			79	82	82
TOTAL			63	61	119	97	129	65	34	140	147	246
AVERAGE			21.0	61.0	39.7	48.5	64.5	65.0	34.0	70.0	73.5	61.5
			6	9	13	18	23	34	40	60	73	
Gore	15.5.62	100	40	42	70	90	96	96	96	96		96
	"	60	43	47	74	84	89	91	93	93	95	95
	"	74	36	38	49	62	67	70	73	73		73
	"	100	29	33	47	49	54	59	61	63	64	64
	"	90	20	21	34	48	50	50	50	51		51
	"	30	30	33	40	50	50	50	50	57		57
	"	100	29	33	45	58	64	68	70	71	72	72
TOTAL			227	247	359	441	470	484	493	504	231	508
AVERAGE			32.4	35.3	51.3	63.0	67.1	69.1	70.4	72.0	77.0	72.6
			6	9	13	17	28					
Porter's Pass	14.5.63	100	8	25	48	52	61					61
	"	30	7	23	43	50	60					60
TOTAL			15	48	91	102	121					121
AVERAGE			7.5	24.0	45.5	51.0	60.5					60.5

Overall average germination percentage : 65

*These five localities have been described in detail in Appendix A.

Table 2.3.a Germination percentages of A. odoratum seed.

Island, New Zealand. This was due to a heavy fungus infestation, although thrips infestation might have contributed.

It is very easy to lose one's objectivity when selecting seeds for germination tests. Blind seed can be picked out immediately and even seeds affected by thrips can be removed beforehand. Thus, it is understandable that when ordinary sweet vernal seed is sown in the field or on soil in a laboratory or glasshouse, the actual strike is far less than could be expected from germination tests. Strelkova (1932) says that A. odoratum seeds when left to themselves, y take a long time to germinate, but the process can be speeded up under laboratory conditions by light and temperature. In pots with sandy soil germination begins in 7 - 10 days, in ploughed nursery soil after 5 weeks and in heavy clay soil after the winter (all seeds were sown at the same time in July). She obtains the following germination rates: 97% in pots, 74% in nursery soil and only a few % in heavy clay. When germinated in soil, soil and aerial microorganisms will influence the strike of the seeds, and subsequent plant establishment. W. Davies obtained 18.5 percent establishment of viable A. odoratum seed sown in a field trial at Aberystwyth, compared to 32.9 percent for Lolium perenne (Stapledon et al., 1927). It was observed that when broadcast on soil, young seedlings of A. odoratum were not as badly affected by fungi as those of Holcus lanatus in a dense stand. The coumarin content of the A. odoratum seedling may prevent fungal attack to some degree. Coumarin is an antifungal substance. For other physiological properties see Chapter 8.

It has been noticed that sweet vernal seed germinates as soon as it is shed from the panicle, if the conditions for germination are right. This has been confirmed by

Figure 2.3.A Seedlings at base of parent plant

Strelkova (l.c.). Some of the seed may require cold treatment because another peak in germination occurs in the following spring. Braun-Blanquet (1913, quoted in Schröter, 1926) also found this in the Swiss Alps, but he may have been looking at A. alpinum, which, being an alpine plant, is likely to require cold treatment for germination. I found that A. alpinum "seed" from Saas Fee, Switzerland, germinated and grew in a refrigerator where the average temperature was about -4°C.

Although all seeds used in the germination tests were exposed to light, field observations showed that they would germinate in fairly low light conditions, at the base of parent plants (see Figure 2.3.A) and even within snow-tussocks (Chionochloa rigida (Raoul) Zotov). Kummer (1932, quoted by Stiles (1950)) found that A. odoratum seed germinated only with difficulty in the dark. Figure 2.3.A shows, also that although coumarins are present in the soil near a sweet vernal plant, this does not prevent germination. In fact, French workers have found that it will speed up germination, although coumarins are usually regarded as germination inhibitors (see Chapter 8).

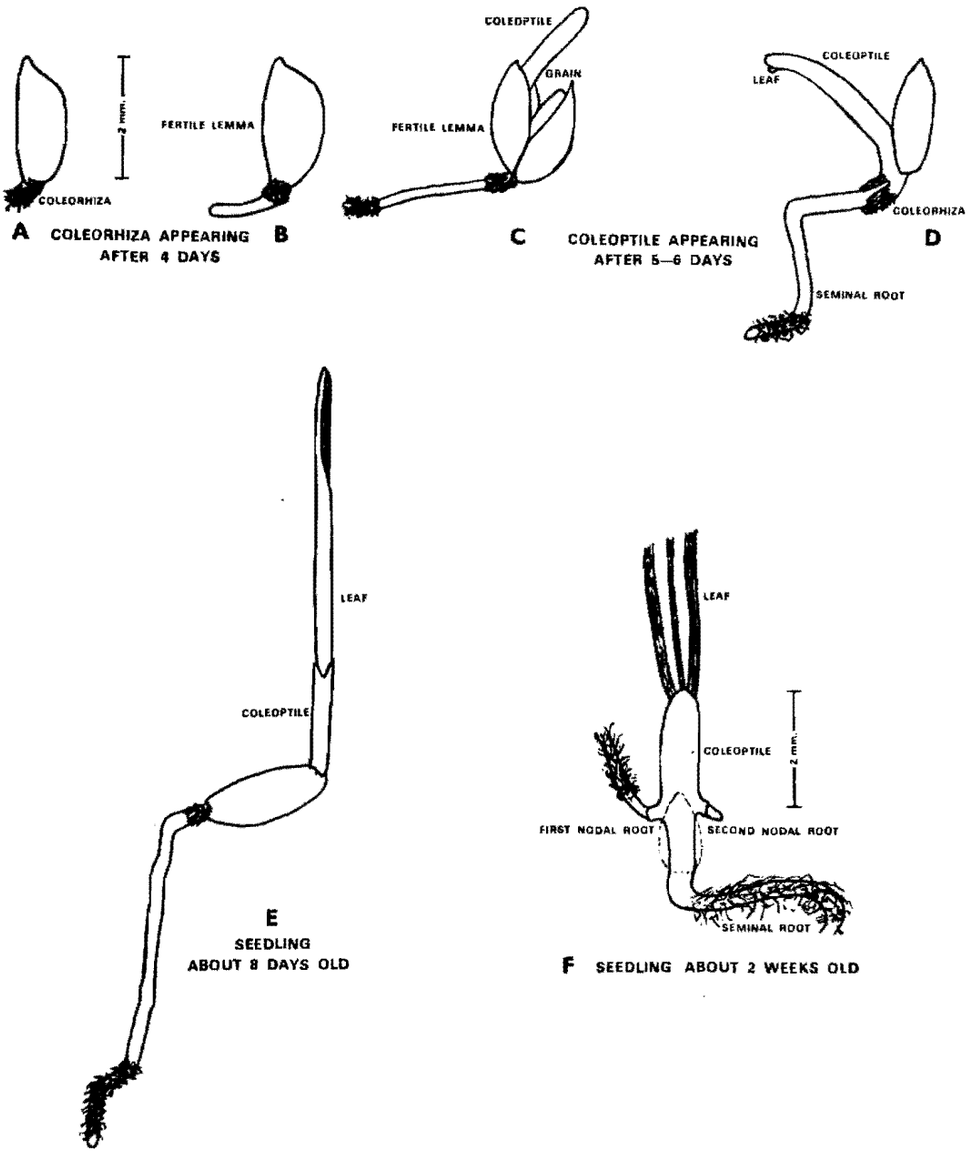
2.4 SEEDLING DEVELOPMENT

To study the early development of the plant, seeds were placed on Whatman germination disks. When the seed germinates after about 4 days, the coleorhiza, which bursts through the fertile lemma, is produced first (Figure 2.4.A, B); a day later the coleoptile appears from the tip of the fertile lemma (Figure 2.4.C, D) which generally stays around the grain. By this time the primary or seminal root has broken through the coleorhiza. The first leaf then breaks through the coleoptile (Figure 2.4.E) and in ten days' time this

leaf may be 19 mm long. In nearly all cases the coleorhiza and primary root develop ahead of the coleoptile and the first leaf. This may enable sweet vernal to become established quickly during this critical period of development. Adventitious or nodal roots are formed in one plane initially (Figure 2.4.F) but later on a whorl of roots can be seen on a node, probably the coleoptilar node (Figure 2.4.G, detail). The extent and fineness of the roots is shown in Figures 2.4.G and H, but it should be pointed out that these plants were grown in sand, without the addition of fertilizers, and in fairly low light conditions (late autumn). The plants shown in Figures 2.4.G and H are 4 to 6 weeks old.

The development of the seedlings from the four localities (Kaikohe, Te Awa, Lincoln, Gore) was studied by measuring the length of the blades at approximately weekly intervals. The seeds were put down for germination on filter paper in petri dishes in the second week of May 1962. As soon as the seedlings could be manipulated, they were transferred to silversand in 8 cm plastic pots and fertilized with complete Hoagland solution. The seedlings were put in a glass cabinet and illuminated with two 500 W tungsten filament lamps, 40 cm from the plants from 9 a.m. to 6 p.m. Four weeks after sowing the seedlings were transferred to boxes filled with sterilized potting soil and put in a glasshouse without additional light. The last two measurements were done on 25 individual plants, the earlier measurements are averages from 30 to 80 plants with two to seven replicates per population. For these reasons, the data were not statistically treated; they have been represented graphically in Figure 2.4.I.

The growth curves of the leaves show the sigmoid shape or part thereof common to all growing leaves or



Figures 2.4.A-F Seedling development in low light.

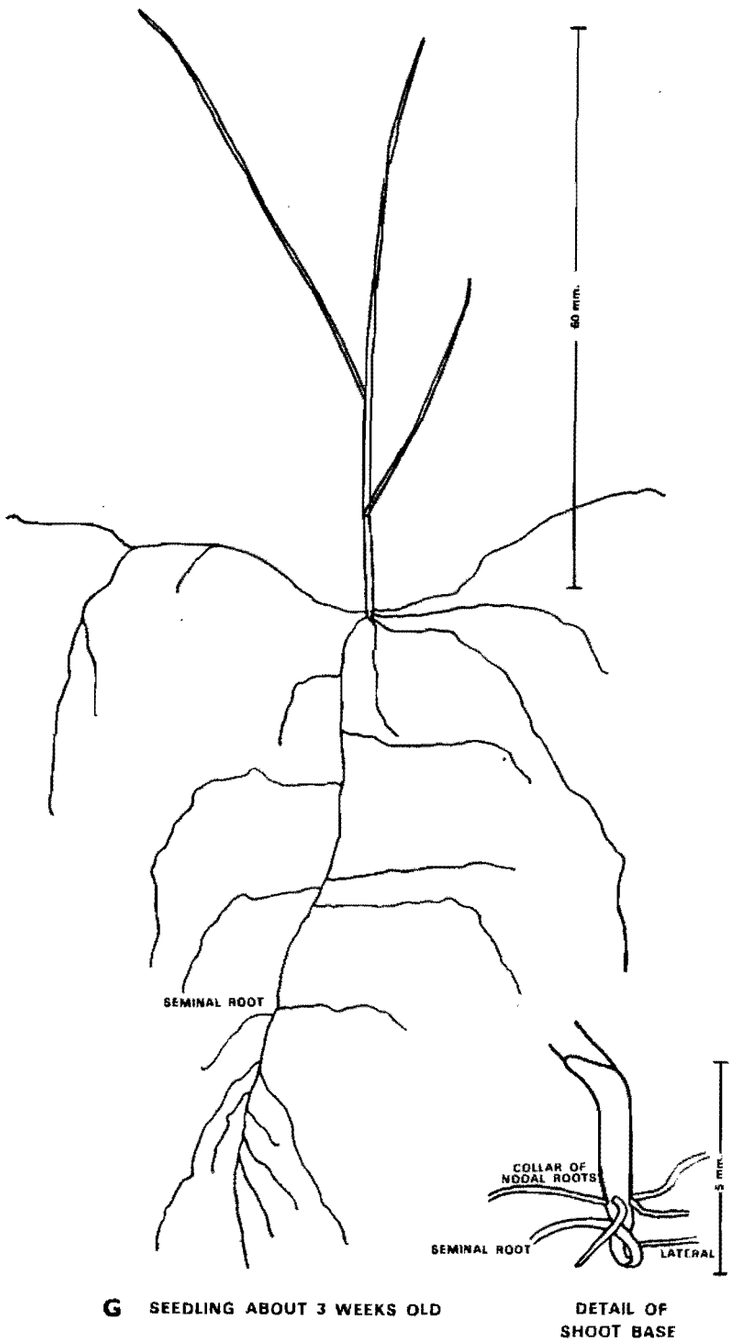


Figure 2.4.G Seedling about 3 weeks old (grown in low light).

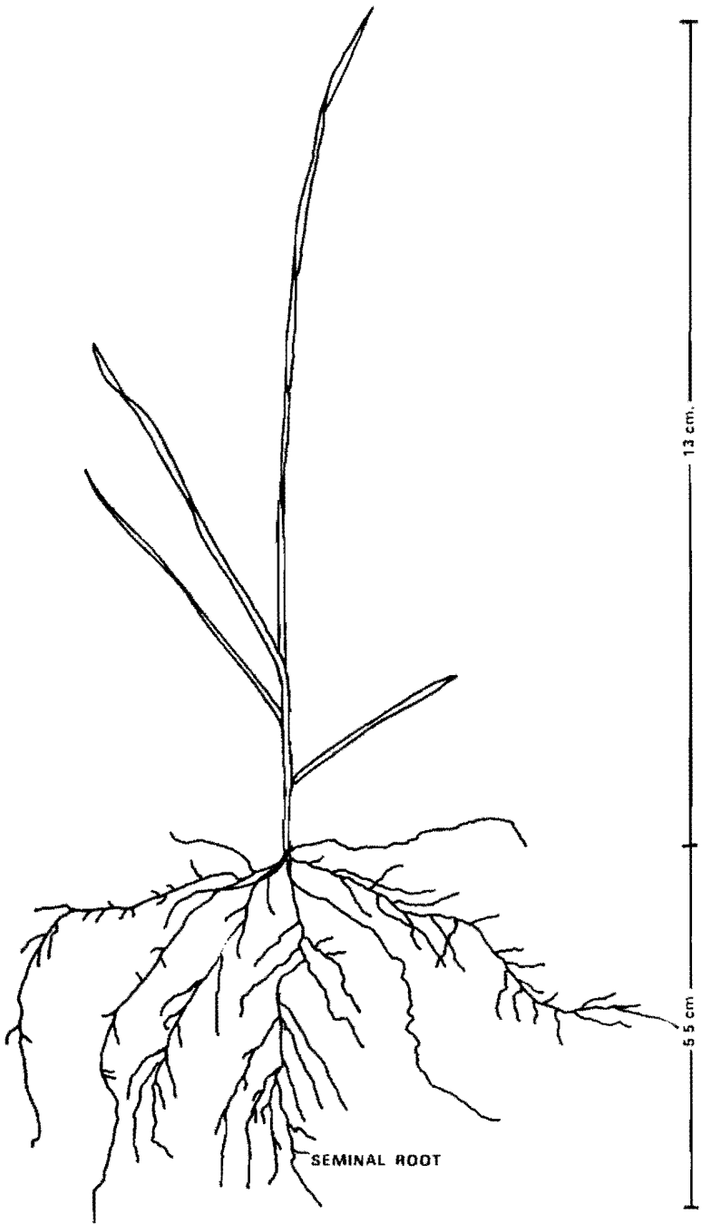


Figure 2.4.H Seedling about 5 weeks old (grown in low light).

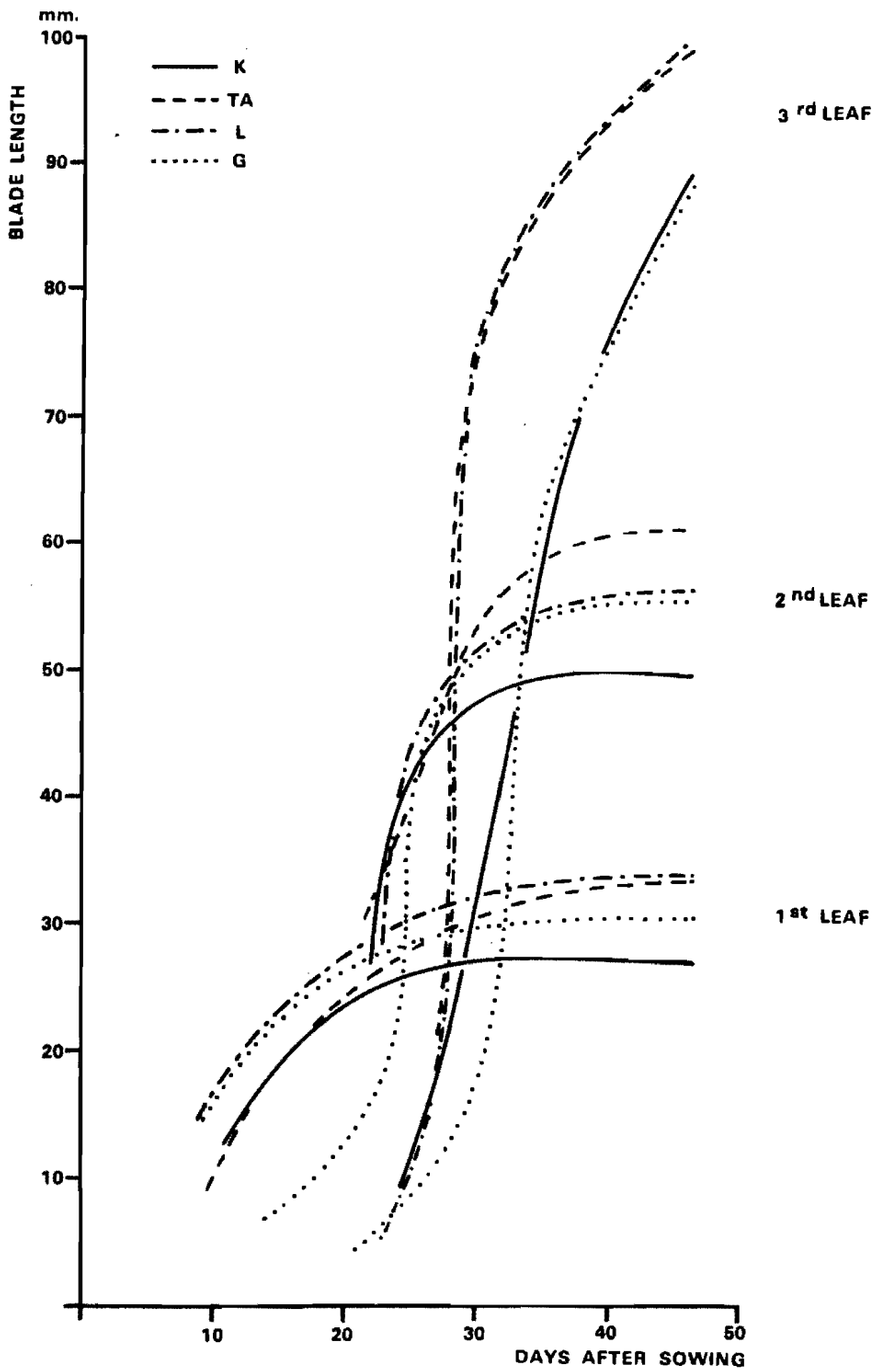


Figure 2.4.I Blade development of seedlings from four localities in New Zealand (K = Kaikohe, TA = Te Awa, L = Lincoln, G = Gore). For description of localities, see Appendix A.

roots when plotted in this manner.

The first point recorded for leaf I is that of total plant height, which is the length of blade plus sheath. It is therefore in excess of the remaining measurements which are of the blade only. If the curves for leaf I were corrected, they would dip more markedly, indicating more rapid growth.

It is clear from Figure 2.4.I that the growth of leaf I has nearly stopped 25 days after sowing when the leaf is 30 mm long; for leaf II the figures are 37 days and 55 mm, and for leaf III, it occurs after more than 50 days when the leaf is more than 100 mm long. The data for leaf IV are not shown but form a straight line; the leaf is about 6 mm long 37 days after sowing and about 90 mm long 8 days later. No measurements were taken after that date. The rapid development greatly assists the seedling to survive this critical period of establishment.

There are differences in growth rates and leaf sizes between the seedlings from the four localities, but since the curves are based on average figures only, and since the variability among the seedlings was large, no significance was attached to them.

When the fifth leaf is between 25 and 50 mm long, the first tiller appears under the experimental conditions described before; it takes place about 53 days after sowing. Very few plants have two tillers at that time.

Occasionally seedlings were observed which lacked any chlorophyll, and once or twice two coleoptiles, giving rise to a twin plant, were formed from one caryopsis.

2.5 TILLER FORMATION

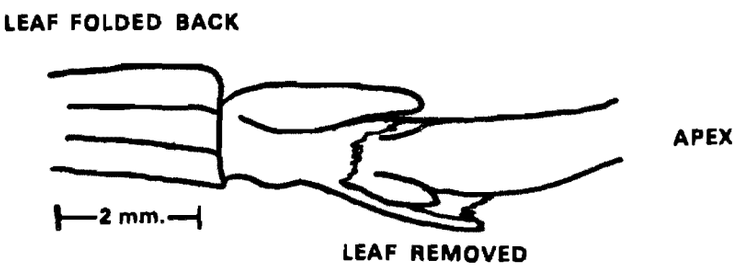
Axillary growth in A. odoratum gives rise to tillers which grow upwards. The result is a tufted or caespitose

Figure 2.5.A Stolon formation on plant TA.16 under moist, low light glasshouse conditions.

plant. No stolons or rhizomes have been observed except by Strelkova (1932) who says that: "In the woods it is a typically rhizomatous grass with a chain of small bushy plants along a horizontal rootstock (Figure 4)". Under glasshouse conditions of low light and high humidity, it was shown that stolons could be formed by internode elongation as is demonstrated in Figure 2.5.A. Under normal conditions extensive internode elongation does not occur, although some elongation takes place in the centre of dense, old plants.

Strelkova (l.c.) states that: "New shoots are always developed extravaginally. New shoots develop intravaginally only when the blade of the old shoot deflects too much from the stem (Figure 2)". This applies to seedlings as shown in her Figure 2, when the plant still has enough room to expand without competition from neighbouring plants. As soon as a plants has more than about 20 tillers, intravaginal tillering occurs also. This gives rise to the characteristic caespitose habit of A. odoratum plants. Figure 2.5.B shows that many tillers are formed intravaginally. Kirchner et al. (1909) stress that intravaginal tiller formation is the rule for the upper buds, which are inside the caespitose plant. The lower buds, which are on the periphery of the plant, break through the leaf sheath, but then bend upwards so that no rhizomes are formed. Observations on single plants in experimental plots confirmed this.

From data based on the botanical analysis of 1647 old permanent grasslands, De Vries and Hoogers (1959) showed that the pattern of tiller distribution of plant species varied with different types of use. In pure hayfields sweet vernal had least tendency to form a caespitose plant but in pastures which were grazed



INTRAVAGINAL TILLER FORMATION

Figure 2.5.B Intravaginal tiller formation in Anthoxanthum odoratum.

only, or occasionally used for haymaking, a distinct tendency could be observed. Sweet vernal did not react as strongly to different types of use as e.g. cocksfoot and perennial ryegrass; this might support evidence for the adaptability of sweet vernal grass.

Tiller formation occurs at a very rapid rate as shown below in Table 2.5.a by Stapledon et al. (1927, Table 9). They sowed several grasses in boxes on 28.2.1923, and on 13.6.1923 individual plants were planted out singly. For comparison the tiller numbers of cocksfoot and perennial ryegrass are shown too:

TABLE 2.5.a Number of tillers per plant

(From Stapledon et al., 1927, Table 9).

Date:		16.4.'23	13.6.'23	22.8.'23	9.5.'24.
Sweet vernal grass		1.9	18.0	214	785
Cocksfoot	Commercial	1.0	5.2	73	105
	Indigenous	1.6	8.1	152	211
Perennial Ryegrass	Commercial	2.0	14.9	388	443
	Indigenous	1.7	18.3	445	557

The very noticeable increase in tiller number during the winter period was confirmed by field observations. Plants consisting of four tillers, were put in the field in September and by next spring these plants had many hundreds of tillers; the majority had become fertile tillers by then.

The change from sterile to fertile tillers occurs in spring but the exact moment, as shown by the "double ridge" formation, could not be determined. However, in early September most apices had panicles in various

stages of development. Sharman (1960) who made a study of the development of the inflorescence and spikelets of A. odoratum says that the change-over from a long, purely vegetative apex to a young inflorescence, is extremely rapid, and so far it has proved impossible to find the presumed intermediate stage with small bud primordia each subtended by its smaller collar-like leaf primordium (i.e. the so-called "double ridge" stage), which is so characteristic of inflorescence initiation and so easily found in grasses such as Agropyron, Triticum, etc.

Once an apex has produced a panicle, it stops growth but apices in the axils of the basal culm leaves can produce new sterile tillers which may then flower in the next spring. Kruyne (1958) also found in Lolium perenne that fertile shoots died back to the node which formed sterile shoots only. Although sterile tillers are formed at the base of old culms, this process does not continue indefinitely, so that old plants die in the centre as has been observed in the field by Böcher (1961) during biosystematical work on Dactylis and Anthoxanthum and by Philipson (1937) for Agrostis setacea Curtis. My own observations on Anthoxanthum odoratum confirm this. Sweet vernal plants with dead centres were frequently invaded by Agrostis tenuis which sometimes lead to complete disappearance of the former.

Even as a very small plant, A. odoratum can survive the winter. Seeds lodged in soil cracks, germinated in autumn and formed only a few tillers possibly due to overcrowding (see Figure 2.10.B). 661 plants had an average of 2.05 tillers on 10 August 1964. Some of these plants flowered that spring, but the majority remained vegetative and increased its tiller number.

Strelkova (l.c.) makes the following observations on the overwintering of the growing points of A. odoratum: "The position of the overwintering buds points in most

cases to the fact that Anthoxanthum odoratum in the central region of the U.S.S.R. is a hemicryptophyte. According to Gam's observations in the Alps (at 2,180 and 2,700 m) on summits where the snow is blown away, the plant is a geophyte and according to our observations it is a chamaephyte when environmental conditions are favourable to its development. The geophytic and hemicryptophytic tendencies of the plant in the first two instances can be explained by climatic conditions; in the third case (the chamaephytic class) the explanation lies in the microclimatic conditions, as a large tussock with thick foliage shelters its buds and creates different overwintering conditions. Thus, judging by the overwintering characteristics A. odoratum cannot belong to a single Raunkiaer class and this emphasizes once again its great plasticity and adaptability".

The longevity of tillers under very low fertility conditions was shown by plants which were broken up into 4 tiller clumps. These stayed alive in pure horticultural sand from April till September; they were watered only. Some clumps had formed a few new tillers. In September they were planted out in the field.

2.6 REQUIREMENTS FOR FLOWERING

2.6.1 Introduction

The stimuli which are necessary to change the vegetative apex of a grass into a reproductive one, vary in kind and in intensity. Frequently, they are inter-related. Once the apex has received the stimulus to become a reproductive one, different stimuli can have different effects on subsequent development. Cooper (1952) has recognized three stages in the development of the inflorescence of grasses:

(1) attainment of competence Most temperate grasses require exposure to low temperatures to attain the reproductive phase but short-day treatment at high temperatures can also induce attainment of competence.

(2) initiation of the inflorescence Once competence is attained, photoperiod will usually be the limiting factor in spikelet initiation. Flowering may occur directly in response to long-day conditions in some grasses or after initial treatment with short-days followed by transfer to long photoperiods in others.

(3) elongation and differentiation of the inflorescence After ear initiation has occurred outdoors in the spring, the photoperiod is lengthening and the rate of development of the inflorescence is limited mainly by temperature. If, however, photoperiod is not allowed to increase regularly, it may be the factor limiting rate of development.

The only studies which have been carried out on A. odoratum to determine the effect of environmental factors on inflorescence development, are those of Tincker (1925). On the basis of his data, sweet vernal grass has been regarded as a long-day plant by Evans (1964). Tincker's data will be discussed below but it was felt that they did not show that A. odoratum was a long-day plant.

In the field, sweet vernal flowers mainly in spring and sometimes in autumn, although Stapledon and Davies (1930) have reported that it will flower through the summer period until well into autumn. This would suggest that the photoperiodic requirements are not very critical and that once ear initiation has occurred, temperature and soil moisture (especially the absence of summer drought) may determine the length of the

flowering season. Therefore experiments have been carried out to determine the effect of day length and temperature on inflorescence development.

2.6.2 Tincker's experiment

Tincker (1925) reports that long-day treatment accelerates flowering in A. odoratum. At Aberystwyth (Wales), he grew cloned sweet vernal plants in pots and exposed them for various lengths of time to natural daylight. To shade the plants they were moved into an open-ended hut so that outside air still had access. This enabled the plants to receive cold treatment for floral induction. The light treatments commenced on 1 February. His experimental results are based on two plants:

TABLE 2.6.2.a Anthoxanthum odoratum. Sweet-vernal vernal grass. Ref. No.15, Bs 1(3). Table 1 of Tincker (1925).

A. An early broadleaf type:

Treatment	Date of 1st panicle emergence	"Zenith flowering"	Panicle height at 30.7.24.	Panicles produced
Control	25.4.1924	28.5.1924	28"	76
12hrs light	11.5	5.6	15"	70
9 " "	11.5	14.6	5"	35
6 " "	19.5	30.6	12"	12*

*Very poor panicles

B. A later narrow-leaf type:

Treatment	Date of 1st panicle emergence	"Zenith flowering"	Panicle height at 30.7.24	Panicles produced
Control	25.4.1924	28.5.1924	19"	40
12 hrs light	25.4	11.5	29"	35
9 " "	2.5	19.5	10"	18
6 " "	19.5	-	7"	1*

*Poor panicle never produced pollen

"Zenith flowering" is the time when the majority of panicles are producing pollen.

"Panicle height" is probably plant height or average culm length.

From these data, Tincker concluded that, by reducing the length of day, plant A was made to flower later, whereas plant B, at 6 hours light daily, did not flower at all. The 12 hour plants received all the available light until the days had lengthened to beyond 12 hours which does not occur until the middle of March; therefore they behaved approximately like the controls.

Long-day plants require photoperiods of 12 hours or more for flowering although some long-day plants will flower in shorter periods. For example, balsam, Impatiens sp., a long-day plant, has a critical day length of 11 hours below which flowering will not occur. It has its optimum at 13 hours but will flower in daylengths from 11 to 18 hours (Thomas et al., 1960, p.491). Although longer photoperiods improved culm length and culm production of the A. odoratum plants used by Tincker, he has not demonstrated that sweet vernal is a long-day plant.

In the experiments described below, the effects of temperature and day length on inflorescence development

of A. odoratum have been investigated.

2.6.3 Low temperature requirement

(a) Introduction

Langer (1955) has stated that in many perennial grasses of temperate regions exposure to low temperatures has proved to be a necessary condition for the attainment of the reproductive phase. The artificial exposure to low temperatures is called vernalization and this word is used here in its original sense (Chouard, 1960): "The substitution of chilling of a plant for the natural exposure to winter in order to make possible the initiation of flower primordia later" and not in its derived sense: "any physiological action stimulating the capacity for flowering, whatever the agent".

Tincker (l.c.) exposed the A. odoratum plants in his experiment to low temperatures and found that they flowered. It seems therefore likely that sweet vernal requires cold treatment in order to attain competence. Whether it does require it and, if so, for how long, has been investigated in the following experiments.

(b) Experiment I. Plants kept in heated glasshouse in short-day conditions.

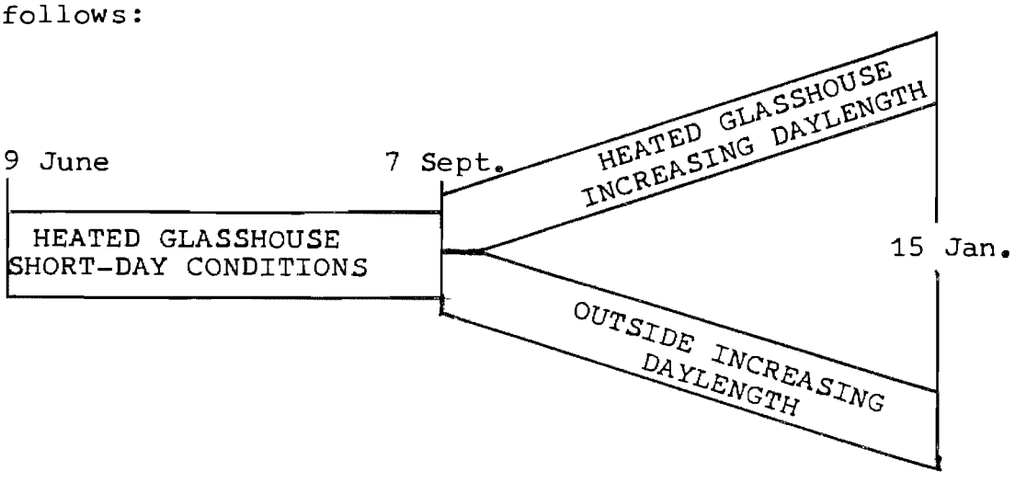
In Section 2.6.1, it has been stated that the attainment of competence can be achieved by short-day treatment at high temperatures. Since it was not known whether A. odoratum would respond to this kind of floral induction the following experiment was carried out.

Seeds were sown in a laboratory on 8 to 10 May 1962 and twentyfive to fortyfive plants per locality were transferred in 15 cm pots to a glasshouse on 9 June 1962 where the maximum temperature ranged from 24°C to 12°C. The glasshouse was in the shade of a building and did not receive any sunlight during the winter months.

Artificial light was given during the day for 9 hours with 5 x 150 W tungsten filament bulbs and 2 x 80W fluorescent tubes, suspended 75 cm above the plants. This additional light from 9 a.m. to 6 p.m. was given until the first week of October when direct sunlight reached the glasshouse. No shading was applied so that the plants were subjected to increasing day length.

On 21 August and on 4 September some apices were examined and were found to be in a vegetative state whereas plants which had been growing in the open all winter had reproductive apices. It appeared that sweet vernal grass requires exposure to low temperatures to attain competence for inflorescence development. Therefore, half of the plants were moved from the glasshouse into the open on 7 September to see whether they could be induced to flower by cold treatment in spite of the lateness of the season.

Schematically the procedure can be represented as follows:



From this procedure information was obtained on:

(1) the effect of short-day photoperiod on the attainment of competence and the effect of increasing daylength on inflorescence development.

(2) the effect of short-day photoperiod followed by low temperature treatment on the attainment of competence and the effect of increasing daylength on inflorescence development.

The results for the plants kept continuously in the heated glasshouse are shown below:

TABLE 2.6.3.a Plants kept in heated glasshouse flowering on 15.1.1963.

Locality*	Plants used	Plants Flowered	Percentage of plants flowering	Av. number of panicles per plant
Kaikohe	12	6	50	9
Te Awa	12	1	8	1
Lincoln	12	1	8	24
Gore	17	2	12	2

*These four localities have been described in detail in Appendix A.

It is clear that the attainment of competence can occur under short-day conditions, especially in Kaikohe plants. Whyte (1948), discussing the work of Gregory and Purvis, and Cooper (1960) found that floral induction can be brought about in Gramineae by short-day treatment at high temperatures. However, it should be pointed out that on a few nights the temperature in the heated glasshouse dropped below +7°C, which is the highest temperature which can still effectively vernalize grasses (Chouard, 1960). The minimum temperatures in June were: 6 nights $<$ + 7°C (2 nights $<$ +5°C); in August: 1 night $<$ + 7°C (0 night $<$ +5°C); in November: 2 nights $<$ + 7°C (0 night $<$ +5°C). This makes a total of 12 nights of less than + 7°, or 2 nights of less than + 5°C. This may have been enough to induce the Kaikohe plants to flower but because of the low numbers of panicles per plant, this induction cannot have been very strong.

It seems that short-day treatment followed by increasing daylength in the absence of cold treatment can induce attainment of competence for inflorescence development.

The results for the plants kept in the heated glasshouse and then transferred to the open on 7 September are shown below:

TABLE 2.6.3.b Plants kept in heated glasshouse from 9 June to 7 September and then transferred to the open flowering on 15.1.1963.

Locality*	Plants used	Plants flowering	Percentage of plants flowering	Av.number of panicles per plant
Kaikohe	13	9	69	38
Te Awa	13	8	61	20
Lincoln	13	8	61	22
Gore	18	11	61	13
Gore**	10	9	90	25

*These four localities have been described in detail in Appendix A.

**All plants from seeds of one panicle.

The minimum temperatures in September were: 15 nights $< 7^{\circ}C$ (9 nights $< 5^{\circ}C$); in October: 7 nights $< 7^{\circ}C$; in November: 5 nights $< 7^{\circ}C$ (1 night $< 5^{\circ}C$) and in December: 2 nights $< 7^{\circ}C$. This makes a total of 29 nights of less than + $7^{\circ}C$, or 10 nights of less than + $5^{\circ}C$. Chouard (1960) quotes that Lolium perenne is easily vernalized by only 15 to 30 days at $5^{\circ}C$ or less. A. odoratum needs even less than 15 days at $5^{\circ}C$ for vernalization as this

experiment shows, although the previous short-day treatment may have had some inductive effect. If the average number of panicles per plant is regarded as an indicator of the cold requirement for floral induction, it is evident that the response to cold treatment is much stronger than the response to short-day photoperiod as shown in Table 2.6.3.a. It is interesting to note that the requirement for cold treatment increases as the plants come from more Southern latitudes. It is remarkable that the plants derived from the seeds of one panicle of a Gore plant, had a small low temperature requirement as shown by its percentage flowering and the average number of panicles. This means that even in the Gore locality plants occur which have a moderate low temperature requirement for flowering. This emphasizes the variability present in A. odoratum populations. Cooper (1960) detected marked differences in inductive requirement between genotypes in outbreeding populations of Lolium.

From Experiment I, it is concluded that:

(1) short-day treatment at high temperatures has a small effect on the attainment of competence

(2) short-day treatment at high temperatures followed by 10 nights of less than $+5^{o}C$ has a distinct effect on the attainment of competence for inflorescence development.

(c) Experiment II. Plants kept in heated glasshouse in natural photoperiod

This experiment was conducted to test the impression gained from the previous one that sweet vernal plants from Southern latitudes have a higher cold requirement for floral induction than plants from Northern latitudes. If this impression could be confirmed, it would support

Cooper's (1960) findings of marked differences in inductive requirement between genotypes in outbreeding populations of Lolium, which have been in their habitats undoubtedly for centuries, whereas A. odoratum has been in New Zealand for about one hundred years only.

Approximately 25 plants from seed from four localities and only 5 plants from the fifth locality (Porter's Pass) were kept in 15 cm pots in a heated glasshouse for a whole winter from the middle of February 1963 till the end of the experiment. No light treatments were given. The maximum temperature in the glasshouse fluctuated from approximately 24°C to 10°C during the winter period but one night in February and six nights in March had a minimum temperature of less than 7°C (one night in February and four in March of less than 5°C). Since the thermometer was about four metres from the plants, it is possible that the temperatures near the plants were somewhat lower, as the plants were arranged at the end of a glasshouse (see Figure 2.6.3.A). This could explain the high percentage of flowering plants although they were rearranged fortnightly. They were inspected on the following dates:

TABLE 2.6.3.c Plants flowering in heated glasshouse in natural photoperiod. Put in glasshouse in middle of February 1963.

A = Number of flowering plants;
B = Average number of panicles per plant.

Locality*	Plants used		1963			1964		Percentage of flowering plants
			9.11	26.11	10.12	3.1	10.4	
Kaikohe	25	A	8	15	18	21	21	84
		B	3.4	13.7	20.8	29.1	40.4	
Te Awa	25	A	4	9	12	13	14	56
		B	3.5	9.7	15.3	21.8	25.7	
Lincoln	21	A	6	10	11	12	12	57
		B	5.0	10.5	17.2	20.7	21.7	
Gore	25	A	-	4	6	10	10	40
		B	-	2.3	5.5	5.8	7.4	
Porter's Pass	5	A	-	2	3	3	3	60
		B	-	1.0	5.7	15.7	21.3	

*These localities have been described in Appendix A.

Figure 2.6.3.A Flowering plants which had been in heated glasshouse in winter. (Photo taken 2-11-1963.)

There is a definite decrease in the average number of panicles per plant and in the percentage of flowering plants as the populations come from further south. This means that the more northern populations have a smaller low temperature requirement than the southern plants. Cooper (1960, 1963) observed a similar physiological response among climatic races of Dactylis and Lolium from various parts of Europe, which he studied at Aberystwyth, Wales. In Section 3.2, it will be mentioned that most introductions of A. odoratum into New Zealand (a little over one hundred years ago) have been from Great Britain and only a few from various parts of Europe. Thus, the A. odoratum plants at the various collection sites can not be expected to be as physiologically distinct as the climatic races used by Cooper (l.c.) which might have been for centuries in the various localities; this is why the physiological responses he obtained were more decisive than the ones presented in Table 2.6.3.c. The possible existence of climatic races of A. odoratum in New Zealand will be discussed in greater detail in Chapters 5 and 10.

From Experiment II it is concluded that among A. odoratum plants from different localities in New Zealand there is a distinct latitudinal gradient in the cold requirement for floral induction.

(d) Experiment III. Plants kept in heated glasshouse in long-day conditions

Simultaneously with Experiment I plants were kept in a heated glasshouse in long-day conditions to find out whether these conditions would produce floral induction.

It was thought that the plants from the Gore locality (45^{o} 52' S.L.) would respond more readily to long-day conditions than those from Kaikohe (35^{o} 26' S.L.).

Therefore only seed collected at the Gore locality was used in this experiment.

The seed was sown on 15 May 1962. The plants were transferred to a glasshouse on 16 and 23 June 1962 in two batches of 25 plants, each plant in a 15 cm pot. 6 x 150 W tungsten filament bulbs and 2 x 80 W fluorescent tubes suspended 120 cm above the plants provided additional light for long-day conditions of 16 hours. The light from this glasshouse could not affect the plants treated in Experiment I.

The result of this experiment was that none of the 50 plants had flowered by 16 January 1963. The low temperatures recorded in August (seven nights with less than 7°C; only two nights with less than 5°C) and in September (two nights with less than 7°C; none less than 5°C), did not appear to have vernalized these plants. When Petkus winter rye was grown in long-day conditions at 18°C by Gregory and Purvis (see Whyte, 1948), they found that it flowered in the following autumn. It is possible that the A. odoratum plants used in this experiment would have flowered then also but they were not kept for such a long period.

From Experiment III it is concluded that competence for inflorescence development cannot be induced by long-day conditions.

(e) Conclusions

From the three Experiments described in this Section, it is concluded that:

(1) A. odoratum has a definite low temperature requirement. This requirement is about 10 days at +5°C when preceded by 3 months of short-day treatment.

(2) this low-temperature requirement shows a latitudinal gradient and increases for A. odoratum plants from more southern latitutdes.

(3) short-day treatment at high temperatures has some effect on the attainment of competence for inflorescence development.

(4) long-day treatment at high temperatures does not induce attainment of competence.

Although these three experiments have not demonstrated that A. odoratum is not a long-day plant, it is suggested that further research into the effect of daylength on inflorescence initiation may show that this grass has a very low photoperiodic threshold because of its earliness of heading. It may simulate S24, an early flowering strain of Lolium perenne, which had reached its threshold early in spring with a photoperiod of 11-12 hours (Cooper, 1952).

2.7 PANICLE EMERGENCE AND FLOWERING

2.7.1 Panicle emergence

Panicle emergence was studied on plants established from seed and from direct transplants at the experimental grounds at Ilam of the Botany Department, University of Canterbury. For the direct transplants, plants were obtained from five localities in New Zealand - Kaikohe, Te Awa, Lincoln, Gore and Porter's Pass (for description of sites see Appendix A). These will be referred to as "Block A". Seed was obtained from only four localities (Porter's Pass excepted) and the plants established from this seed will be referred to as "Block B". These plants have also been used for morphological studies described in Chapter 7 where more details can be found about planting arrangement and management. Block A was planted on 22 May 1962 and Block B on 25 August 1962.

On each plant in both blocks, all panicles were counted and classified as:

"H", panicles without stigmata or stamens,

"S", panicles with stigmata but without stamens,

"A", panicles with stigmata and stamens.

This was done in 1962 on block B and in 1963 on blocks A and B. The counting dates are shown in Table 2.7.1.a and in Figures 2.7.1.A to C. The figures have been derived from the data in brackets in Table 2.7.1.a. These data have been obtained as follows: H: number of plants with panicles "H" (see above) expressed as a fraction of the total number of plants; S: number of plants with panicles "S" expressed as a fraction of the number of plants with panicles "H" on the same date; A: number of plants with panicles "A" expressed as a fraction of the number of plants with panicles "H" on the same date. Average number of culms is the total number of culms divided by the number of flowering plants at each date. When the culm number exceeded 100 per plant, the figure has been estimated from the number of culms counted at the end of December in each year for the morphological studies described in Chapter 7.

Figure 2.7.1.A shows that the sequence for panicle emergence (panicles H) is initially in latitudinal order: the plants from the furthest north flower more intensely and at an earlier date than those from furthest south but on 25.11.62 and at subsequent dates the Lincoln plants flower more intensely than all other plants. A latitudinal sequence can also be observed in the average number of culms per plant but at later dates the number of culms on the Lincoln plants drops. In Chapter 5, Experiment A, more examples and an explanation of this phenomenon will be given. The lines for panicles S and A show a small but distinct advance of S over A. This illustrates the protogynous character of Anthoxanthum odoratum which will be discussed in more detail in the

BLOCK A (DIRECT TRANSPLANTS)

LOCALITIES*	Kaikohe		Te Awa		Lincoln		Gore		Porter's Pass	
DATE: 5-10-1963										
"H"	18	.35	1	.09	27	.82	0	0	7	.32
"S"	3	.17	0	0	1	.04	0	0	0	0
"A"	2	.11	0	0	1	.04	0	0	0	0
HEADS	6.3		4.0		17.6		0		14.3	
DATE: 14-10-1963										
"H"	41	.80	4	.37	32	.97	4	.33	19	.86
"S"	13	.32	3	.75	18	.56	1	.25	4	.21
"A"	8	.20	0	0	11	.34	0	0	1	.05
HEADS	34.2		6.0		71.2		2.3		37.4	
DATE: 23-10-1963										
"H"	51	1.0	11	1.0	33	1.0	6	.5	21	.95
"S"	48	.94	6	.55	32	.97	5	.83	20	.95
"A"	43	.84	3	.27	31	.94	5	.83	17	.81
HEADS	86.1		23.4		111.0		38.0		89.8	
DATE: 2-11-1963										
"H"	51	1.0	11	1.0	33	1.0	9	.75	22	1.0
"S"	51	1.0	11	1.0	33	1.0	9	1.0	21	.95
"A"	51	1.0	11	1.0	32	.97	9	1.0	20	.91
HEADS	200.0		78.1		143.0		77.7		168.0	
NO.OF PLANTS MEASURED	51		11		33		12		22	

BLOCK B (PLANTS FROM SEED)

LOCALITIES*	Kaikohe		Te Awa		Lincoln		Gore		Kaikohe		Te Awa		Lincoln		Gore	
DATE: 3-11-1962									DATE: 5-10-1963							
"H"	13	.58	3	.14	8	.36	0	0	3	.14	1	.05	9	.41	0	0
"S"	7	.54	1	.33	6	.75	0	0	0	0	0	0	0	0	0	0
"A"	1	.08	0	0	2	.25	0	0	0	0	0	0	0	0	0	0
HEADS	2.8		5.0		3.4		0		9.7		13.0		19.2		0	
DATE: 25-11-1962									DATE: 15-10-1963							
"H"	19	.86	12	.55	20	.91	9	.41	17	.77	5	.23	18	.82	4	.18
"S"	19	1.0	12	1.0	20	1.0	9	1.0	2	.12	1	.2	6	.33	0	0
"A"	18	.95	10	.83	17	.85	7	.78	2	.12	1	.2	4	.22	0	0
HEADS	9.5		8.1		6.4		5.3		37.0		25.0		48.8		5.8	
DATE: 4-12-1962									DATE: 24-10-1963							
"H"	19	.86	17	.77	22	1.0	11	.5	22	1.0	17	.77	22	1.0	20	.91
"S"	19	1.0	17	1.0	21	.95	10	.91	20	.91	6	.35	20	.91	10	.5
"A"	19	1.0	15	.88	20	.91	9	.82	14	.64	5	.29	18	.82	4	.2
HEADS	14.9		10.4		8.0		9.3		88.0		23.6		76.7		34.8	
DATE: 19-12-1962									DATE: 3-11-1963							
"H"	20	.91	18	.82	22	1.0	15	.68	22	1.0	18	.82	22	1.0	22	1.0
"S"	20	1.0	18	1.0	22	1.0	15	1.0	22	1.0	17	.94	22	1.0	22	1.0
"A"	20	1.0	18	1.0	22	1.0	13	.87	20	.91	14	.78	21	.96	20	.91
HEADS	18.4		13.6		9.2		10.1		199.0		66.2		115.8		146.2	
NO.OF PLANTS MEASURED	22		22		22		22		22		22		22		22	

Figures not underlined:

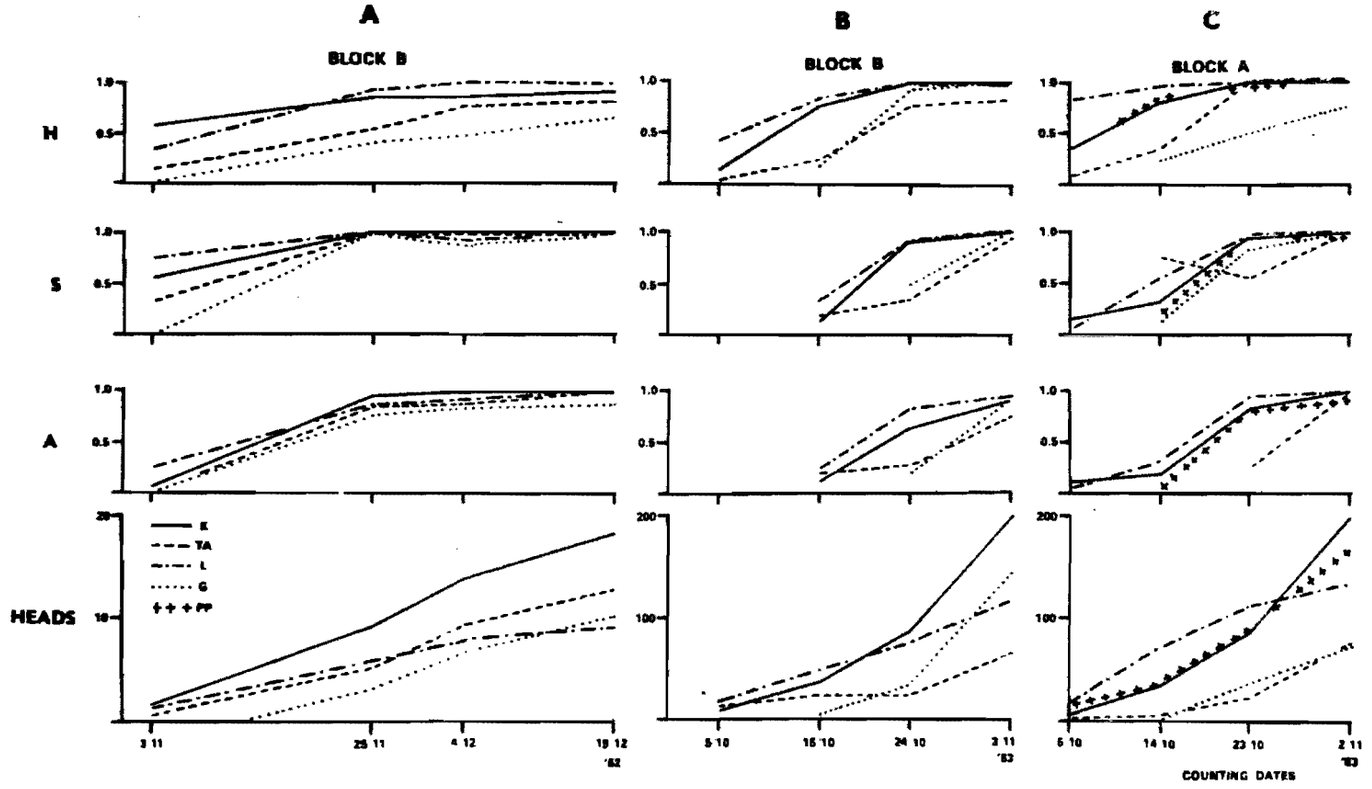
"H" : Panicles without stigmata or stamens
"S" : Panicles with stigmata but without stamens
"A" : Panicles with stigmata and stamens
HEADS : Average number of panicles per flowering plant

Figures underlined:

H : Number of plants with panicles "H" (see above expressed as a fraction of the total number of plants
S : Number of plants with panicles "S" expressed as a fraction of the number of plants with panicles "H" on the same date
A : Number of plants with panicles "A" expressed as a fraction of the number of plants with panicles "H" on the same date

*These localities have been described in Appendix A.

Table 2.7.1.a Panicle development



Figures 2.7.1.A-C Panicle development in the field. (Block B 1962, Block B 1963, Block A 1963). H, S, A based on underlined figures in Table 3.7.1.a. HEADS = average number of panicles per flowering plant. K = Kaikohe, TA = Te Awa, L = Lincoln, G = Gore, PP = Porter's Pass. These five localities have been described in Appendix A.

second half of this section. These lines also show a nearly latitudinal sequence except for the Lincoln plants. It is likely that these plants which had been planted out about three months before, were still better adapted to the local Ilam environment than the plants from other parts of New Zealand. This suggests that a factor other than daylength has a pronounced effect on panicle emergence in A. odoratum; this factor may be temperature as has been found for Lolium by Cooper (1952) and for Phleum pratense by Ryle and Langer (1963). It may be demonstrated in Figure 2.7.1.D which shows a plant with pronounced panicle emergence on its sunny side. Many similar plants have been observed. They had been trimmed back in late autumn.

Figure 2.7.1.B shows that the sequence for panicle emergence (panicles H) for the plants from the localities K, TA, and G is initially in latitudinal order with the exception of the Lincoln plants. As suggested above, the latter may be better adapted to the local environment than the plants from the other localities. The average number of culms per plant shows the late flowering of the Gore plants which may be a day length effect, and the low culm numbers of the Te Awa plants which suggests low vitality. This may be due to the seed from which the latter were raised: It was collected at the end of the flowering season and such seed may have less vitality. From the lines for panicles S and A, the protogynous character of sweet vernal is again clear although on the last date this is not distinct any longer.

Figure 2.7.1.C shows that there is some latitudinal sequence for panicle emergence (panicles H) but the plants from the localities L and PP form exceptions. The previously suggested explanation for the behaviour of the L plants may again be put forward but the similarity

in behaviour of the PP and the K plants seems rather strange. However, it is suggested that given more favourable temperatures, montane plants (PP) will flower as abundantly as vigorous lowland plants (L or K), and that this is important in a montane environment where conditions favourable for flowering may be of such short duration that intensive flowering is necessary to ensure survival of the species. That the plants at the Porter's Pass site were found to have few culms and tillers does not negate this suggestion: it only shows that in spite of adverse conditions the genes for vigorous flowering and tiller production have not been lost. The temperatures at Ilam may have enhanced panicle emergence in the PP plants but depressed it in the K plants, which resulted in apparently similar behaviour but this may be purely coincidental. The low average culm number of the TA and G plants may be due to their age, and the drop in the final count of L culms may show that in spite of their vigour as single plants, they do not seem to have the capacity to produce as many tillers (and culms) as the K and PP plants. This in turn may be a left-over from the habitat of the Lincoln plants which favoured plants with few but tall culms. The protogynous character of sweet vernal is not very distinct in these older plants established as direct transplants. In the plants established from seed (Block B) and thus younger, protogyny was more evident but on the whole protogyny seems to be of little value in the outbreeder A. odoratum and it may be just a trait inherited from one of its parents.

From Figures 2.7.1.A to C and probably D, it is clear that both daylength and temperature affect panicle emergence in A. odoratum, but no attempt has been made to separate these two factors. Ryle and Langer (l.c.), having studied Phleum pratense, stress that the control of

Figure 2.7.1.D Effect of light and temperature on panicle development. (Midday-sun on left; photo taken 15-10-1963.)

the stages leading to flowering is complex.

2.7.2 Flowering

Flowering in A. odoratum has been described in detail by Beddows (1931). It starts at the apex of the panicle and proceeds downwards. Since the floret has no lodicules, it opens very slightly but just enough to allow the stigmata and anthers to pass between the tips of the lemmas. The stigmata, long and feathery, are exserted some time before the anthers; thus A. odoratum is a protogynous plant as has been observed by many botanists (see Beddows l.c.). Kirchner et al. (1909) say that this protogyny is frequently so distinct that the panicle appears to be first wholly pistillate before it becomes staminate. Usually the stamens start to appear at the apex when the stigmata are visible half way down the panicle. The two large anthers emerge together from the floret. They are mostly yellow but a purplish colouration has been observed occasionally; when they have become pendulous on the long filaments, pollen is liberated. Cross pollination is therefore the most common type of fertilization for A. odoratum. Sometimes self-fertilization occurs as has been observed by Beddows (l.c.), Strelkova (1932) and Borrill (1963). This was confirmed in the following experiment:

Plants were taken from a single plant block at Ilam, Christchurch, and transferred to 25 cm pots which were placed in a glasshouse. Panicles which did not show any stigmata were isolated using the normal bagging technique with lunchpaper and cottonwool plugs. Certain plants produced stigmata before the panicles had completely emerged from the leaf sheath; this presented difficulties when bagging but they were overcome by removing the culm blade and by raising the bagged panicle as the culm elongated.

TABLE 2.7.2.a Analysis of selfed panicles

Locality*	Plant Number	Panicles bagged	Average Panicle Length in mm	Average Total Seeds	Average Fertile Seeds**	Self Fertility Percentage
Kaikohe	14	6	57.8	42.0	0.50	1.2
	19	4	64.8	67.5	1.75	2.6
Te Awa	5	7	69.0	63.6	1.29	1.6
	24	7	63.0	74.7	0.29	0.4
Lincoln	1	6	61.7	76.8	0	0
	5	6	71.8	44.0	0.14	0.4
Gore	13	6	58.8	69.8	0.16	0.2
	15	6	57.3	70.7	0.33	0.5
Dry Creek	24	5	76.0	106.2	0	0
	30	6	63.0	83.2	0.16	0.2

*These localities have been described in Appendix A.

**For definition of "fertile seeds" see Section 2.9.

It is clear from these figures that some self-fertilization does occur in A. odoratum, especially in the populations from northern localities. Of the 59 bagged panicles, 4 had set seed when stigmata were just visible, 13 had set seed although stigmata were not visible (which shows that self-fertilization occurs) and 8 had set no seed when stigmata were just visible. Self-fertilization is thus of little importance and A. odoratum must be regarded as a cross-fertilizing plant.

To test cross-fertilization one plant each was taken from two populations growing in the single plant block mentioned before. One panicle was selected from each plant, and these were put together in a paperbag (similar to the one described for the selfing experiment) before stigmata were visible. One panicle set seed well (53 fertile seeds from a total of 92), but the other very poorly (9 fertile seeds from a total of 110) which suggested that only the pollen from one plant could successfully fertilize the ovaries of the other. The significance of this single cross is limited; no further crosses were made because of practical difficulties. However, it seems incorrect for Kirchner et al. (1909) to say that not only self-fertilization but even cross-fertilization within the same stand is without success, just because Koernicke found that a few panicles in that stand were completely sterile.

Flowering occurs in Ilam from the middle of October; the spikelets are shed at the end of December. This corresponds roughly with the observation of Sinclair (1824) in England: it comes to flower in April and the "seed" is ripe generally about the first or second week of June. De Vries (1941b) made similar observations in the Netherlands:- flowering in the middle of May,

shedding of spikelets in the middle of June. Autumn flowering has been observed in the plants at Ilam but no viable seed was formed.

2.8 POLLEN VIABILITY

The pollen grains are round and whitish, have a diameter of 14 μ, are densely covered with small warts, so that the grains are not transparent (Warnstorf, quoted by Kirchner et al. 1909).

By using the differential staining method of Owczarzak (1952) the functional and aborted pollen grains were determined in eight different plants. Two hundred grains were observed per plant; it was found that the functional pollen percentage is over 90 in panicles which have just started flowering to 50% in panicles which have nearly finished flowering. These high figures promote the possibility of successful wind pollination.

2.9 SEED SETTING

Panicles which had been freely pollinated were bagged before the spikelets were shed, to assess the seed produced per panicle.

Fertile seeds are those which cannot be squashed flat between tweezers. They are rounded, fully ripened and likely to be viable. Sterile seeds are those which can be squashed flat between tweezers. The caryopsis has not been formed or has been eaten by thrips (see plant K 25).

The variability among the 17 bagged panicles limits the significance of the figures in Table 2.9.a. Therefore, the average number of fertile seeds per millimeter of panicle, which is 1.2, is the only figure that will be discussed. It may seem a low figure but many

TABLE 2.9.a Seed production per panicle

Plant		Date bagged	Fertile seeds	Sterile seeds	Total seeds	Ratio Fertile / Sterile	Percentage fertile seeds	Panicle length in mm	Seeds per mm of panicle	Fertile seeds per mm of panicle	Comments
K 25	I	3.1.63	65	184	249	.35	26	68	3.7		Approx. 60% of sterile seeds infested by thrips.
	II	"	30	196	226	.15	13	66	3.4		-do- 80%
	III	"	16	211	227	.08	7	73	3.1		-do- 70%
TA23	I	"	204	64	268	3.19	76	65	4.1		
	II	8.1.63	163	58	221	2.81	74	67	3.3		
	III	"	130	64	194	2.03	67	55	3.5		
L 21	I	3.1.63	52	31	83	1.68	63	90	0.9		
L 23	I	"	31	45	76	0.69	41	55	1.4		
G 7	I	"	72	48	120	1.50	60	43	2.8		
	II	"	70	50	120	1.40	58	40	3.0		
	III	"	75	30	105	2.50	71	41	2.6		
G 14	I	"	123	134	257	0.92	48	89	2.9		
	II	"	93	89	182	1.04	51	86	2.1		
	III	"	107	100	207	1.07	52	82	2.5		
G 23	I	"	59	125	184	0.47	32	78	2.4		
	II	"	41	106	147	0.39	28	81	1.8		
	III	"	60	96	156	0.63	38	82	1.9		
Total			1,391	1,631	3,022			1,161			
Average			81.8	95.9	177.8	0.85	46	68.3	2.6	1.2	

K = Kaikohe, TA = Te Awa, L = Lincoln, G = Gore. These localities have been described in Appendix A.

panicles are produced per plant; 930 were counted on a two and a half year old single plant which was the highest figure obtained. The average length of the panicles of this plant was 50.4 mm. Such a plant may therefore produce 56,246 fertile seeds which is ample to enable a plant to maintain itself in a community. It also enables a plant to colonize new areas.

The average number of fertile seeds per plant from the population of 22 single plants, which included this plant with 930 panicles, was 29,761. This is a much higher figure than that of 966 reported by Rozanova (1925b) for plants growing in a "derelict field", fallow arable land. It is likely that those plants were also growing as single plants in that field but they might have been younger and thus had fewer panicles. Kirchner et al. (1909) state that the A. odoratum tussocks stay fairly small and support this with Scharlock's find of a tussock with 59 culms, implying that this is quite a large number. It appears then that growing as a single plant favours sweet vernal, which suggests that it is a colonizer that cannot stand competition. This has been found frequently in the literature and during field observations.

This figure of 29,761 fertile seeds per plant is very high when compared with other weedy plants. The following figures are from Korsmo (1930) unless stated otherwise.

Table 2.9.b shows that under very favourable circumstances A. odoratum can produce as much seed as several troublesome weeds. This enables it to colonize areas where the microsites for establishment (Harper, 1960) are suitable. The early ripening of the panicles and the instantaneous shedding of the spikelets, give A. odoratum a distinct advantage in hayfields where the

TABLE 2.9.b Seed numbers per plant

Botanical Name	Average figure	Range	Authority - Remarks
Agropyron repens	50*		*per spike
Agrostis setacea		250 - 300*	Ivimey-Cook (1959), *per panicle.
Alopecurus myosuroides		40 - 400	
Anthoxanthum odoratum		64 - 966	Rozanova (1925b)
" "		100 - 56,000	Lambrechtsen
Arrhenatherum elatius		750 - 3,000	Pfitzenmeyer (1962)
Avena fatua	450		
Bromus mollis	1,600	few 100 - 1,800	
" secalinus		730 - 1,450	
Lolium temulentum	300		
Nardus stricta	2,000*		Chadwick (1960), *clump 20 cm in diameter.
Poa annua	450		
Achillea millefolium	3,300		
Capsella bursa-pastoris		2,000 - 40,000	
Cerastium holosteoides	1,200		
Chenopodium album	3,100	few 100 - 20,000	
Cirsium arvense	4,600	3,500 - 40,000	
" palustre	7,000		
" vulgare	2,800		
Prunella vulgaris	350		
Rumex acetosella		1,000 - 10,000	
Solanum nigrum	40,000		
Sonchus oleraceus	4,700	up to - 25,000	
Taraxacum officinale	3,000		
Juncus conglomeratus	4,500*		*per stalk
" effusus	6,000*		*per stalk

seed of most grasses has not been shed yet when the fields are mown. In these circumstances more seed will be shed from sweet vernal than from the associate grasses which enables sweet vernal to increase in low fertility hay-fields or laxly grazed pastures. If it is mown before seeding for a few years, it will disappear; it has to shed seed to maintain itself in a stand of vegetation. Where soil fertility is high, other grasses increase vegetatively more rapidly than sweet vernal, which will be suppressed and decrease. It is therefore not found on strongly growing leys (Kirchner et al., 1909).

Field observations suggest that at high altitudes the late start of the growth season and the occurrence of late frosts affect flowering and seed setting. This temperature effect may determine the altitudinal limit of A. odoratum. However, plants were found to set seed at 1,300 m at Mt Cockayne, Craigieburn Range, Canterbury on an eroded site, at 1,550 m at Mt Misery, Black Range, Canterbury on a moist well-grassed site, and at 1,370 m on the Black Birch Range, Marlborough on a fairly eroded site (see Section 5.9.2). Low light appears to prevent seed setting in shaded localities and during autumn flowering.

2.10 SEED DISPERSAL

It has been said already that the spikelets of A. odoratum are shed as soon as they are mature. Kirchner et al. (l.c.) describe in detail how the spikelet wriggles out of the glumes until it sits on their tips: there the wind or occasionally animals or man brushing past them, can carry the spikelet away. Its long barbed awn and hairy spikelet easily hook on to skins of animals and probably even birds so that animals may contribute markedly to the distribution of A. odoratum seed. Field

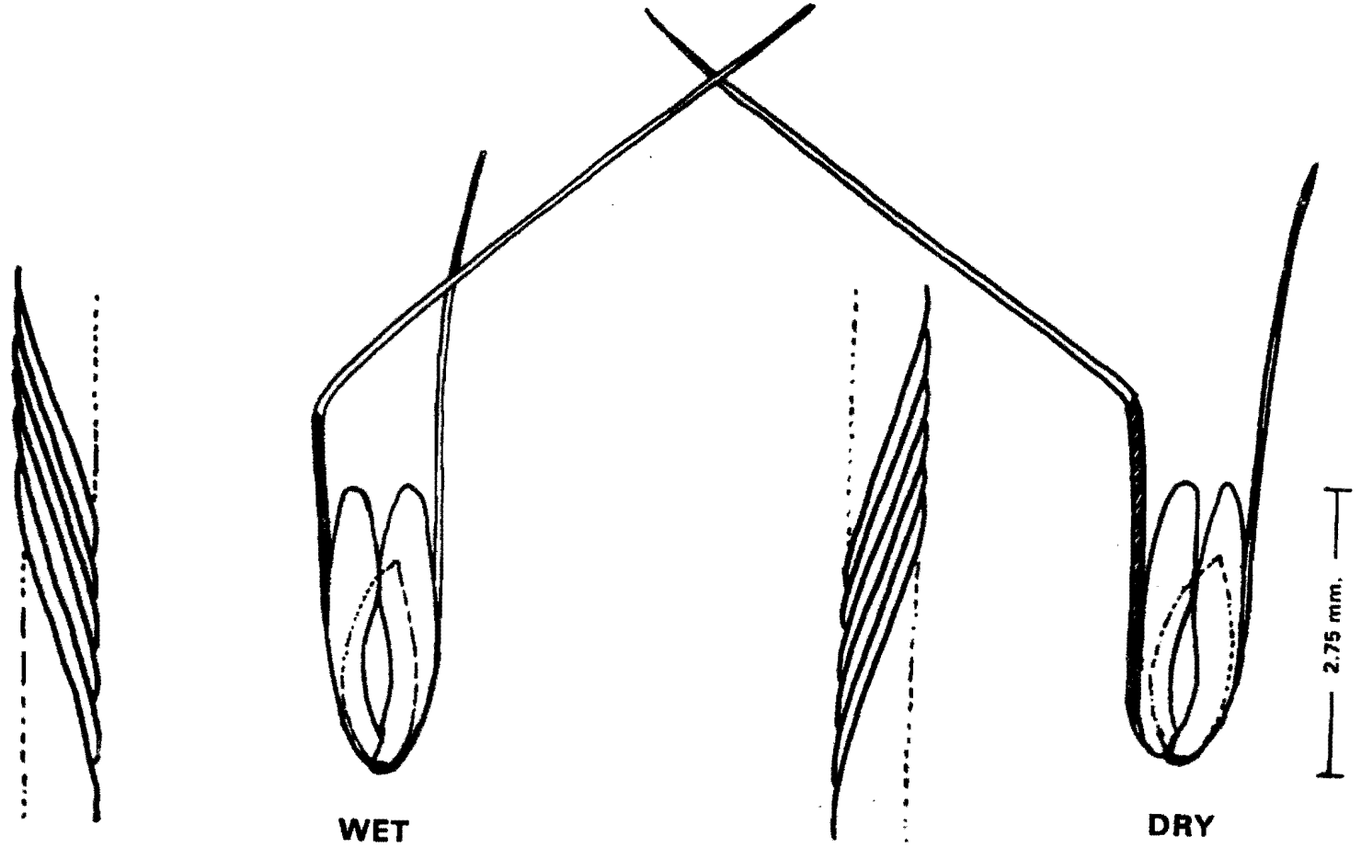


Figure 2.10.A Effect of moisture on spiral in bent awn. (Hairs omitted from lemmas.)

Figure 2.10.B Seedlings developing in soil cracks.
(Photo taken 17-7-1964.)

observations suggest that wind especially in mountain regions, may also be very important as a dispersal agent since A. odoratum has a light seed (see Section 2.2) and since plants are sometimes found in very isolated localities. However, its effect as a dispersal agent has not been determined. Early settlers may have spread sweet vernal very rapidly in New Zealand as they frequently carried a bag of seed to scatter around on their travels and even on their musters.

The number of spikelets which had been shed onto the ground, was counted in a block of single plants arranged in a 60 x 60 cm planting grid at Ilam. Before the spikelets were shed, the vegetation between the plants had been skimmed off leaving a smooth surface. Halfway between two plants, the following figures were obtained on 100 cm^2: 350, 220, 200. The counts were made on 31 December 1962 when most of the panicles were empty. In view of the large number of seeds produced per plant, it was not surprising that these counts were obtained from a small area. The figures are only approximations as many spikelets may have disappeared into the cracks that had formed in the soil.

The long awn on the upper sterile lemma of the spikelet enables it to wriggle into soil cracks and crevices and other micro-sites which may be suitable for establishment. This awn has a hygroscopic spiral just below the "elbow" in the awn. The spiral consists like a rope of individual strands which are connected at either end but not interconnected. It will change into the opposite direction when moistened or dried as shown in Figure 2.10.A, flicking the spikelet about in the process. In this way the spikelet can jump up to 75 mm (average of five spikelets: 26 mm) on filterpaper and may bury itself in soil crevices in the field. That

the spikelets become established in soil cracks is shown by Figure 2.10.B. Kirchner et al. (1909) also describe the movements of the spikelet in great detail but they doubt whether the movements are of any significance in establishment since they are so erratic.

The more rapid establishment of awned "seeds" versus de-awned "seeds" was shown for Danthonia penicillata (now Notodanthonia penicillata (Labill.) Zotov) by Simpson (1952). Six months after sowing, seedlings from the awned seeds numbered twelve times as many as those from the de-awned. When sweet vernal spikelets are de-awned by removing the sterile lemmas, the seed becomes completely immobile, but it may still roll or be splashed by rain into sites suitable for establishment, since it is a light seed. Germinating sweet vernal seeds appear to have few demands on their environment, as long as sufficient moisture is available. Seedlings stayed alive for three months on Whatman germination pads, while receiving only distilled water.

2.11 SEED LONGEVITY

The seed of A. odoratum remains viable for several years when stored in brown paper bags on a laboratory shelf at room temperatures, as shown by Table 2.11.a. The sterile lemmas of the spikelet were removed and the seeds were germinated without pre-treatment in petrie dishes on Whatman germination pads at room temperatures and natural lighting conditions.

Table 2.11.a shows that most seed germinates within five weeks after sowing and that the germination percentage is not much lower than that for fresh seed as shown in Table 2.3.a. However, the percentages for the Dry Creek and Te Anau localities are very low. The former appeared to be badly infected by bacteria

TABLE 2.11.a Germination percentages of "old seed" of Anthoxanthum odoratum

Locality*	Date of collection	Date of sowing	Number of seeds used	Inspection dates in days after sowing								Total germn. %age	Fungal infection %age	Thrips infection %age	Blind seed %age
				11	17	23	36	50	60	79	96				
Kaikohe	11. 1.63	23.3.66	100	41	17	4	9	1	1	1	-	74	9	2	15
	14. 2.63	23.3.66	100	2	34	38	4	1	-	-	-	79	16	5	-
	14. 2.63	23.3.66	100	1	34	34	4	-	1	1	-	75	4	5	16
Te Awa	17. 1.63	22.3.66	100	24	19	14	8	1	5	-	-	71	21	-	8
Lincoln	14. 2.63	23.3.66	100	3	29	35	-	-	-	-	-	67	9	5	19
	9.12.63	22.3.66	93	17	25	43	4	3	1	-	-	93	6	1	-
Gore	23. 2.63	22.3.66	100	8	33	8	1	-	1	-	-	51	33	5	11
Porter's Pass	18. 1.63	22.3.66	97	6	29	35	7	2	-	-	1	80	9	4	7
Dry Creek	28.12.63	21.3.66	100	7	8	3	3	-	1	-	-	22	8	2	68
Te Anau	6. 1.62	21.3.66	100	-	-	6	3	1	-	1	-	11	3	20	66

*These localities (except Te Anau) have been described in Appendix A. The Te Anau sample was collected along the road to Milford on the boundary of the township.

whereas the latter was infested with thrips; the seed was also a whole year older than that of the other samples. This might have reduced the germination percentage still further.

Kirchner et al. (1909) state that the germination percentage of A. odoratum seed drops slowly: after one year by 5%, after two by 15% and after three by 35% of the original germination percentage. If this statement is based on results from similarly stored seeds, then it is not confirmed by the above figures.

Harris (1961) showed that sweet vernal seed, sown in the field, germinated both in autumn and in spring and even in the next autumn. This prolonged emergence supports the finding that the seed remains viable for a number of years. Further support comes from the work of Chippindale and Milton (1934) who determined the number of viable seeds present in soil under pasture. Although the number of sweet vernal tillers present in the pastures was mostly only one percent of the total vegetation, one to 26 seeds which produced seedlings were found in the top inch of soil in an area of 15 x 15 cm. In soil under pastures established on formerly arable land, viable sweet vernal seed was frequently found at considerable depth: four to five inches below the surface. It could be that the viable seed found at this depth had been taken there by soil organisms such as earthworms, beetles, ants or even moles, but it could also have been ploughed under before the pasture was established. Some pastures were 40 to 50 years old but still contained viable seed in the subsoil. In a survey of pastures in Wales, Milton (1936) recorded up to 2.5 million sweet vernal seeds per acre in fields with swards up to five years old, and up to 4.5 million seeds per acre in fields with swards more than five years old. This "seed store" in the soil is

of importance when the vegetation is disturbed or removed.

2.12 ROOTS AND OTHER UNDERGROUND ORGANS

The functions of the root system are anchorage, absorption of water and minerals, and storage of food reserves. The first two functions are the main ones of the roots of A. odoratum. Fleshy roots or other underground organs were never observed among its fine, fibrous roots and it is unlikely that they are important as storage organs. Strelkova (1932) is the only worker who observed rhizome formation in A. odoratum (see her Figure 4). Kirchner et al. (1909) mention "rhizomes" which accumulate graminin and some starch; they specify the buds and terrestrial leaf sheaths as storage organs. It appears that they use the word "rhizome" for any part of the shoot which is in the soil and do not restrict it to a subterranean, stemlike organ which forms roots at its nodes, has scales when young and serves mainly for vegetative reproduction of the plant (Kruyne, 1958). I have never observed any rhizome formation. However, under low light conditions in a glasshouse some plants form roots at the nodes of tillers with strongly elongated internodes; these elongated tillers simulate stolons (see Figure 2.5.A).

A. odoratum has very fine fibrous roots which penetrate the soil very rapidly but not very deeply. Overnight root growth of two centimetres by newly formed adventitious roots was observed on washed plants left in wet newspaper at room temperature. Under field conditions root growth is undoubtedly less rapid. For depth of rooting, Troughton (1957) quotes the figure of one metre for 18 months' old plants with most roots going down to about 50 centimetres.

The roots are mostly thin ($<$ 0.2 mm diameter) and have a persistent cortex. Kirchner et al. (l.c.) describe how with increasing age of the root, all elements of the xylem, the pericycle and especially the endodermis get strongly thickened cell walls. This may explain the hard, felty clump of roots which is formed after a few years. The effective absorption surface of such a clump of roots may become so small that it cannot support the aerial part of the plant any longer and this may cause the plant to die (W.A. Jacques, pers. comm.). This may be the reason for the limited perenniality of A. odoratum plants (Kirchner et al. (l.c.); Böcher, 1961) and hence its need for an effective means of sexual reproduction (see Section 2.9). Troughton (l.c.) quotes Klapp's (1934) figures who finds a root dry weight per hectare of 8,627 kg for the plant combination A. odoratum/Festuca ovina. The root distribution figures for the same plant combination (measured as dry weight and expressed as a percentage) in a soil under a mountain heath sward (Calluna/Antennaria association), moderately grazed, are as follows:

0 - 10 cm : 66.8%;
10 - 20 cm : 17.3%;
20 - 30 cm : 9.1%;
30 - 40 cm : 4.4%;
40 - 50 cm : 2.4%.

The same rapid decrease was observed in the field whenever plants were dug up. It is shown in Figure 2.12.A. This 4 months' old plant was growing in a friable, infertile silt loam. On 14 April 1965 (when it was photographed) it had 153 tillers, shoot dry weight was 18.2 g, root dry weight was 4.9 g. The plant was suspended in a narrow perspex tank, 20 cm high. The very dense clump of roots is evident. It is likely that these numerous fine roots

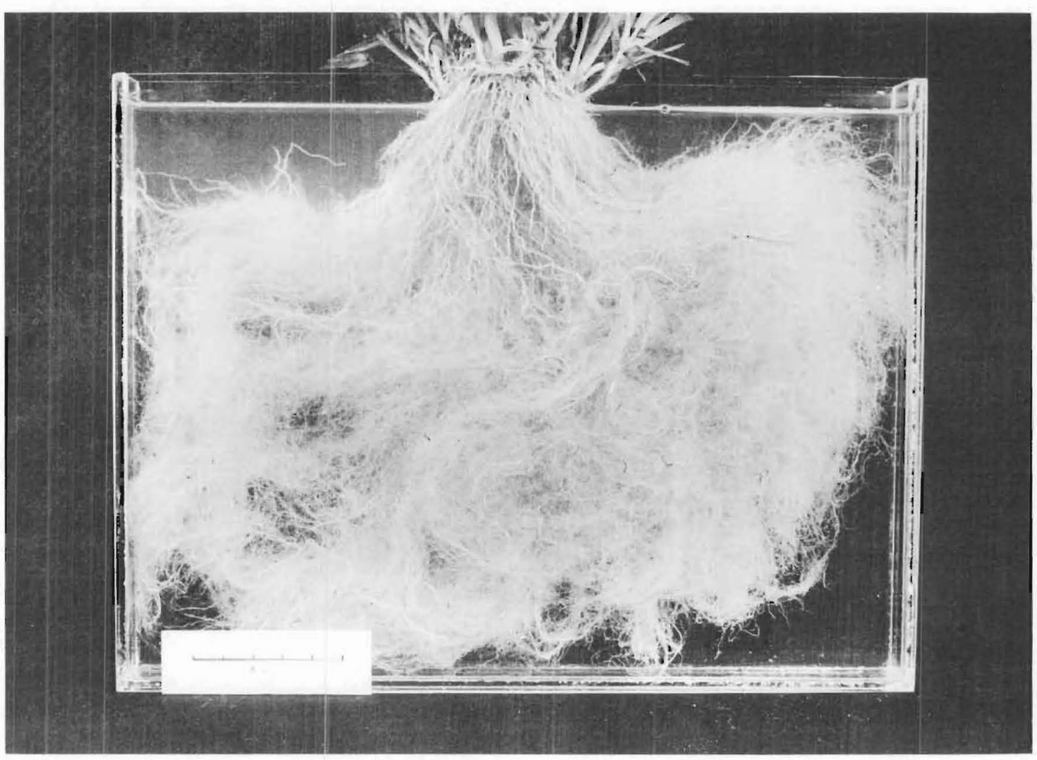


Figure 2.12.A Roots in narrow perspex tank, 20 cm. high. Plant 4 months old.

enable A. odoratum to absorb sufficient minerals for growth even from low fertility soils, but being shallow-rooting, it is susceptible to drought.

The colour and thickness of roots varies with temperature, moisture, and to some extent with soil fertility and light (Soper, 1957). It was observed that in moist pots and in a uniform potting mixture, the plants growing at low temperatures (10°C) had thick white roots (up to 1 mm in diameter) especially at 1,500 fc. as compared to 800 fc. But when the plants were growing at high temperatures (25°C) and low light (800 fc.), the roots were brown and did not appear to have actively growing root tips. Soper's (l.c.) findings for Lolium perenne confirmed this.

In common with other grasses (see Troughton l.c.), A. odoratum has a flush of root growth in early spring before leaf growth starts, but root growth also occurs in autumn and winter. At what temperature root growth stopped, was not determined but since seeds germinated in a refrigerator and produced roots, it is likely that root growth might take place at soil temperatures near freezing point as was found by Stuckey (1941) in Rhode Island, U.S.A., for nine temperate grass species (see Troughton l.c.). In summer under drought conditions and at high soil temperatures, root growth stops or is very much slowed down. Under these conditions vegetative growth stops too and plants may die unless they are irrigated.

Figure 2.4.H of a young seedling shows that the seminal root becomes finely branched. Brouwer (p.154, 1966) states that "It is generally recognized that the effectiveness per gramme root weight of the fine seminal roots is much greater than that of the nodal roots". Although it is not known how long the seminal root of

A. odoratum lives it is likely that its rapid growth during the early stages of development of the seedling enables the young plant to become established more successfully. Adventitious or nodal roots are formed in a whorl on the nodes (see detail in Figure 2.4.G) and not on both sides of the lateral buds as occurs in wheat (Percival, 1921, quoted by Brouwer, l.c.).

Gyllenberg (1955) investigated the rhizosphere effect of A. odoratum in virgin soils in Finland. It was found that the number of bacteria was eleven times higher in the rhizosphere of sweet vernal than in the corresponding non-rhizosphere control soils. Phleum pratense and Poa pratensis which were studied at the same time, had higher counts than A. odoratum but the counts for the latter remained fairly constant when the soil pH dropped, whereas those of the former decreased markedly under acid soil conditions. This may imply that A. odoratum is better suited to acid soils which is supported by the findings of Kruyne and de Vries (1963), see Section 4.4.

The roots smell strongly of coumarin which may have some effect on the rhizosphere although it is rapidly broken down by bacteria (see Chapter 8).

2.13 SUMMARY

The life history of A. odoratum has been described in detail and is summarized here:

(1) it has a light "seed",
(2) its "seed" germinates rapidly in light and has no or only a slight dormancy period,
(3) its seedling establishes and develops quickly and has very low environmental requirements,
(4) it forms tillers rapidly,
(5) it has a definite low temperature requirement.

This requirement is about 10 days at +5°C when preceded by 3 months of short-day treatment. There is a latitudinal gradient among plants from different localities for this low temperature requirement; it increases for plants from more Southern latitudes,

(6) short-day treatment at high temperatures has some effect on the attainment of competence for inflorescence development; long-day treatment at high temperatures has no effect,

(7) panicle emergence is influenced by both daylength and temperature,

(8) it has a protogynous flower without lodicules; protogyny is more obvious in seedlings than in 3-4 year old plants; it flowers early,

(9) it has highly functional pollen which assists cross-pollination,

(10) it produces large quantities of seed,

(11) its spikelets are easily dispersed by wind, animals and man,

(12) its seed remains viable in the soil for five years or more,

(13) its fine, fibrous roots permeate the soil rapidly but tend to form a felty clump after about three years; being shallow-rooting, it is susceptible to summer drought,

(14) its perenniality is limited to about three to five years.

CHAPTER 3

AGRICULTURAL IMPORTANCE AND INTRODUCTION INTO NEW ZEALAND

3.1 INTRODUCTION

The agricultural importance of sweet vernal grass in New Zealand has decreased from its original popularity with the early settlers to its present status of a "weed". However, it is abundant in many parts of this country, especially on the low fertility soils of the South Island high country. The recent developments in Great Britain, where low coumarin-high producing strains of sweet vernal are being selected, may be the beginning of renewed agricultural importance of this grass both in New Zealand and in Great Britain. The two phases of agricultural importance are discussed here. The introduction and rapid spread of sweet vernal in New Zealand has also been investigated.

3.1.1 Agricultural importance, pre-1900

Sweet vernal grass was introduced into New Zealand by the European settlers because it was a component of standard English grass mixtures for permanent pastures and was liked for its pleasant smell and early growth which was readily eaten by sheep and cattle. It became permanently established throughout New Zealand, but especially in the South Island high country where it still is of some significance since it provides the first green feed after the winter.

In his famous Hortus Gramineus Woburnensis, Sinclair (1824) gives the following production figures for sweet vernal grass (modified to kg/ha) based on the yields from a plot of four square feet (3,716 cm^2):

Yield on 1st April	3,908 kg/ha
Yield at time of flowering (middle of April)	8,773 kg/ha
Yield when seed is ripe (middle of June)	6,865 kg/ha
Yield of "latter-math"	7,628 kg/ha

Heeger and Poetke (1954) produce more recent figures by quoting Becker-Dillingen (1929) who recorded the following annual yields of sweet vernal grass:

Green matter	from 8,000 to 15,000 kg/ha
Hay	from 3,000 to 5,000 kg/ha
Seed	200 to 300 kg/ha.

Van Itallie (1934) obtained the following dry matter yields from plots sown at the end of April 1932:

Harvest middle July 1932	3,820 kg/ha
Harvest end of May 1933	from 1,910 to 4,630 kg/ha
Harvest end of July 1933	from 1,820 to 1,880 kg/ha.

These production figures are about half those of perennial and italian ryegrass, harvested at the same time. No data are available of autumn growth.

Sinclair (l.c.) observed already that although the chief property that gives merit to sweet vernal is its early growth, it is in this respect inferior to several other species which are later in flowering. He also quotes the work of a Mr Grant of Leighton who put down a large field, one half with sweet vernal grass and white clover, and the other half with meadow foxtail and red clover. It was noted that sheep would not touch the sweet vernal-white clover sward although sweet vernal grew very luxuriantly in this pasture, but went for the meadow foxtail-red clover sward. In a seedsmixture for permanent pastures, Sinclair (l.c.) recommends $\frac{1}{4}$ bushel of sweet vernal grass out of a total of nearly 16 bushels per acre. He works this out at 213 seeds per square foot (about 6 seeds per 100 cm^2) which definitely seems a generous seed

rate, since one big single plant can occupy this space. Sinclair's detailed observations on grasses and his critical assessment of sweet vernal could be the reason that it gradually lost favour with farmers.

In New Zealand sweet vernal started to lose favour by about 1880 when Wilkin (1877) said that he could not recommend it for cultivation. After the closest observation he had been unable to detect any real value in this grass. He thought that it owed its reputation to its agreeable odour. He noted that it was very sparingly eaten by stock, even in early spring when it formed the only green feature in the pasture and, when other grasses were abundant, it was neglected altogether. In the same year Curl (1877) wrote that "Anthoxanthum odoratum grows all the winter, spring and autumn, and is good feeding grass during those seasons." Steel (1889) still called it a useful grass but in 1893 (Anon.) it was included in a list of British weeds occurring in Canterbury and Professor McAlpine (Professor of Botany, New Veterinary College, Edinburgh) "makes merry over treatises which recommend it on the ground that it has a sweet smell" in 1897 (Anon.).

Perhaps the best illustration of sweet vernal becoming a weed, is shown by the following recommended seeds mixtures for Canterbury which in 1851 contained ¼ lb of sweet vernal out of a total mixture of about 26 lbs comprising 15 species, but by 1883 it had been reduced to 7 species, sweet vernal being one of the grasses now excluded (Andersen, 1916). From about this time sweet vernal was no longer included in seeds mixtures on purpose, although it maintained itself in many areas and undoubtedly spread in others.

3.1.2 Agricultural importance, present day

It is only recently that sweet vernal grass has received renewed attention, mainly at the Welsh Plant Breeding Station, Aberystwyth, where Borrill is trying to select low coumarin-high producing strains for hill country in the British Isles (Davies et al., 1962). Milton (1953) claimed that of the hill grasses in Wales, sweet vernal was observed to be one of the most palatable to sheep. At a trial at the Welsh Plant Breeding Station a sward of sweet vernal and some white clover was eaten readily by sheep (Jones, 1959) which seems to contradict the report of Sinclair (l.c.) on the work of Mr Grant, mentioned earlier. Larin et al., (1950) state that in montane regions in Russia sweet vernal is eaten well by sheep, cattle, horses and even deer and geese, but in other areas it is of no importance as a fodder grass. Field observations have shown that sweet vernal is grazed in spring but will be avoided as soon as more palatable grasses are available. Cockayne (1920) made similar observations. The avoidance is possibly linked with the increase in coumarin content as sweet vernal matures, which makes it taste bitter to stock (see Chapter 8). Because of the abundance and persistence of sweet vernal on low fertility soils, its agricultural potential has been assessed in this thesis by a detailed study of its ecology (Chapter 4).

3.2 INTRODUCTION INTO NEW ZEALAND

The earliest documented record which I have been able to locate is that of Mr W. Swainson F.R.S., who grew 25 European grasses including sweet vernal at his homestead Hawkshead in the Hutt Valley in 1847 (Swainson, 1847). Since sweet vernal grass was regarded as a good

pasture grass in those days, there can be no doubt that it was present in most European seeds mixtures brought in by the white settlers. It is very likely that the early missionaries and possibly even whalers introduced it into New Zealand before that date, although it does not occur on one of the earliest lists of New Zealand plants, compiled by Cunningham (Wade, 1842). Phalaris canariensis, undoubtedly an introduced grass, occurs on this list, but sweet vernal grass which is easily recognized, is absent.

It should be stressed that many separate introductions of sweet vernal grass from very different parts of Great Britain and to some extent Europe, occurred in New Zealand. In this way, the early settlers brought a large quantity of different genes of sweet vernal into New Zealand and the subsequent mixing of these genes (A. odoratum is an outbreeder) must have led to extremely vigorous plants which rapidly occupied all sites suitable for establishment. It clearly showed its colonizing characteristics.

Early records confirm the rapid spread of sweet vernal. Hooker (1855) mentions A. odoratum on his list of introduced plants and says in 1864 that it is widely dispersed and has been gathered in a viviparous state at 3 - 4,000 ft on Mt Cook by Haast. Since I was rather amazed that A. odoratum was recorded by Haast so far inland so soon, some investigations were made which showed that the specimen of A. odoratum in the Kew Herbarium, collected by Haast in March 1862, is kept in the "Herbarium Hookerianum 1867" and is numbered 728. The plant is not in a viviparous state, but shows vegetative proliferations of the spikelet. It is most likely that the plant was not collected near Mt Cook, since Haast was the first to be on the Tasman Glacier, although Dobson (who accompanied Haast on this trip) has said that a few shepherds (possibly from Glentanner

Station which was occupied by the Dart brothers in 1858) had been up the Tasman Valley and reported it to end in a wall of rock - the terminal moraine no doubt (McClymont, 1935; Haast, 1948). These shepherds could have taken sweet vernal "seed" as far as this terminal moraine, but no sheep had grazed in the Tasman Valley in 1861 (Haast, l.c.). McClymont (l.c.) also reports that the Birch Hill Station, on which the Hermitage now stands, was first taken up in 1866, but it was not stocked until 1868-69. The specimen of A. odoratum was labelled 728 by Haast and the entry in his list of plants received by J.D. Hooker in June 1862 showed that it was collected on "grassy flats and terraces, 2,000 to 3,500' " which still occur extensively on the eastern side of Lake Pukaki where Haast travelled on his way to Mt Cook and where in my opinion the specimen was collected by Haast. The altitude of the collection site is more likely to have been 2 - 3,000 ft (600 - 900 m.) and not 3 - 4,000 feet.

From the "Transactions of the New Zealand Institute" the following Table 3.2.a can be drawn up to illustrate the spreading of sweet vernal.

In one case sweet vernal grass did not spread very rapidly. Guthrie-Smith (1930) describes how it was sown in 1879 at Tutira, Hawkes Bay, but in half a century it had not moved 400 yards from its birthplace, and there had been no attempt at colonization elsewhere on the station. In an earlier paper, Guthrie-Smith (1907) says that it appeared in the home paddock in 1885 and has been slowly spreading since. After all these years (about 20) only 50 acres had been overrun and there was comparatively little in other parts of the run. But in Canterbury sweet vernal became established quickly in native grasslands (Dixon, 1886). They were burnt annually or even more frequently to produce

TABLE 3.2.a The occurrence of Anthoxanthum odoratum in New Zealand during the early years of colonization

Place of occurrence	Year	References
Possibly present near New Plymouth	1867	Buchanan 1869
Great Barrier Island	1868	Kirk 1868a
Kororarika, Bay of Islands	1868	—— 1868b
Thames Goldfield	1869	—— 1869a
Whole of Province of Auckland	1869	—— 1869b
Province of Canterbury	1871	Armstrong 1871
Miramar Peninsula, Wellington Harbour	1872	Buchanan 1872
ABSENT from Invercargill	1872	Webb 1872
ABSENT from Chatham Islands	1872	Kirk 1872
Province of Otago	1874	Thomson 1874
Kawau Island	1876	Buchanan 1876
Port Nicholson and adjacent district	1877	Kirk 1877a
Bluff Hill	1877	—— 1877b
Okarito, Westland	1877	Hamilton 1878
Islands of Hauraki Gulf	1878	Kirk 1878
ABSENT from Stewart Island	1880	Petrie 1880
Possibly present on Stewart Island	1884	Kirk 1884
ABSENT from Three Kings Islands	1887	Cheeseman 1887a
ABSENT from Kermadec Island	1887	—— 1887b
ABSENT from The Snares	1890	Kirk 1890
North Cape District	1896	Cheeseman 1896
ABSENT from Hikurangi Mountain	1897	Adams 1897
ABSENT from Arthus Pass	1898	Cockayne 1898
Westport District	1906	Townson 1906
Kapiti Island	1907	Cockayne 1907
Stewart Island	1909	—— 1909

fresh palatable growth on the tussocks. Burning was usually followed by oversowing with "bushburn" seed, in most cases a weed infested seeds mixture, which will explain the occurrence of many species of exotic plants naturalized on the upland country in the early years of settlement (Smith, 1903). That most seeds mixtures were rarely true to specifications before seed testing was introduced, is made very clear by de Laune Faunce (1882) and by Anon.(1848). In other words, not only "bushburn" seeds mixtures contained many weedy species but all seeds mixtures introduced by the early settlers must have contained a good deal of "strays" as well, unless the mixtures had been handpicked as is strongly recommended by Anon. (l.c.). Neither he nor de Laune Faunce (l.c.) trust even the most renowned seed merchant. Most of these impure mixtures would have contained sweet vernal grass. From field observations, discussed in more detail in Chapter 4, it can be stated that sweet vernal grass occurs wherever the ground has been disturbed by European settlers and their domestic grazing animals.

3.3 SUMMARY

(1) The agricultural importance of A. odoratum in the last century and at the present day has been reviewed.

(2) A. odoratum was present in New Zealand in 1847, but might have been introduced earlier.

(3) Many separate introductions of A. odoratum into New Zealand occurred which enabled this grass to form a new and varied genepool.

(4) Once introduced, A. odoratum spread rapidly throughout New Zealand and clearly showed its colonizing characteristics.

CHAPTER 4

ECOLOGY

4.1 INTRODUCTION

In Section 3.2, the introduction and rapid spread of A. odoratum in New Zealand have been discussed and in Chapter 2, the life history of this grass has been reviewed and supplemented by new findings, which help to understand its ecology. In this chapter, examples are given of the ecological range of A. odoratum, both in Europe and in New Zealand, which illustrate its ecological adaptability. The reasons for this adaptability are considered to be the hybrid origin of A. odoratum, already discussed in Section 1.5, and various facets of its life history, discussed in Chapter 2. Finally, the place of sweet vernal in various agricultural eco-systems is reviewed.

4.2.1 Ecological range in Europe

Anthoxanthum odoratum is distributed throughout Europe and occupies a very wide ecological range as shown by the following extracts:

Kirchner, Loew, Schröter, 1909: ... distributed throughout Europe from the extreme north at North Cape down to the South of Spain, Sicily, the South of Greece and to North Africa (Morocco, Algeria). It thrives under the most diverse climates from the seashore to the snow zones in the mountains*. It tolerates the long summer-drought of the Mediterranean, as well as the many cold spells of

*In the mountains and in the extreme north, this Anthoxanthum is probably A. alpinum L.& L. not A. odoratum L.

the short summer in the Alps; it survives the raw, long winter of the far north and the Alps under lasting snow cover as well as without this protection, and it is able to withstand competition even in the mild winters of coastal lands and islands. It does not tolerate strong shading and is more common on drier soils than on wetter soils, which it does not avoid altogether. It grows on sands, loam and clay; it has a particular preference for humous soil types and is indifferent to the calcium content of the substratum. It makes very small demands on the nutrient supply of the soil and thrives even on very poor sand and peat. Nevertheless, it occurs frequently on rich soils, but is then easily suppressed by other lush and densely growing plants. This may explain why it disappears usually after heavy fertilizing, especially with nitrogen, and why it does not occur in strongly growing leys either.

It can be found in the following plant formations:

(1) Pastures. Sweet vernal is, next to Festuca rubra, the most common pasture plant. In Swiss pasture studies, it was found in 218 of the 351 one square foot stands investigated (F. rubra in 247) and much more frequently in pastures on dry soils (68% of all stands) than in those on wet soils (19%) and also slightly more common on poor pastures (71%) than on fertilized ones (66%)...

(2) Estuaries and fens. Completely absent from estuaries but fairly common in those fens which which are not too wet. Also frequent on dry peat.

(3) Fell fields and screes. Occurs very rarely on these.

(4) Dunes and heaths. Often on the barren sand of dunes and very frequent on heaths.

(5) Forests and mountain basins. Anthoxanthum avoids the dense shade of beech and spruce forests, but is fairly common in pine and oak forests, and especially in the high mountains in thin stands of larch and Pinus cembra... It is rare in the shade of tall, vigorous herbs in mountain basins.

Schröter, 1926: (European Alps) It is one of the most widely distributed grasses. It occurs on all pastures in mountainous countries, from the richest, shadiest orchards on the flats to the poor sunny matlike pastures and meadows in the high country (... up to 3,045 m. at Piz Forun, Albula, where it still forms seed that germinates according to Braun-Blanquet*), on the wet pastures and reedlands of the plains to the driest rockseams and grass clumps in the mountains, on cow and sheep pastures, as well as grassy gardens, in the shade on the humus of chestnut, beech, fir, larch, Pinus cembra, forests and krummholz scrub, in the burning sun on peat and on sterile sand, on all soil types and geological substrata, from the fertile Lias to the most sterile serpentine, and at every degree of moisture and illumination. (From: Stebler, F.G. and Shröter, C. 1902: Die besten Futterpflanzen. A.N. McAlpine translated an earlier edition of this book into English in 1889).

Strelkova, 1932: (Russia) A. odoratum possesses a very wide ecological range. It can settle in the

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*Braun-Blanquet confirms this in his 1964 publication of "Pflanzensoziologie", Table 67, germination percentage 11% for A. odoratum (is probably A. alpinum L. & L.).

most different habitats and among very different vegetation groups. The usual and most characteristic habitats of A. odoratum are all kinds of meadow communities from very arid to very humid. This grass is very often just one of the many grasses constituting a community and less often it is one of the predominant grasses or one which determines the community. As Kreyer (1916) points out, A. odoratum is mostly encountered on podzolised soils. A. odoratum settles very easily on soils which have been swept by fire and on clearings... In light forests, where A. odoratum is also encountered quite often...; A. odoratum can withstand extreme aridity much better than excessive humidity and invariably dies out in badly swamped meadows, in peat, and Hypnum bogs and in Magnocaricetum. It also dislikes darkness and does not grow in thick forests... A. odoratum is also widespread in many different climatic conditions. Its geographical range is very wide. It can be found from the western coast of Europe to the Trans-Baikal regions and from the Arctic Islands to the steppe belt; further south it moves to the mountains and is quite abundant in the Caucasus. It is absent in the Crimea.

Jansen, 1951: (The Netherlands) Common on all soil types but uncommon in very dry localities. In grasslands preferably on poor, acid, fertilized or unfertilized pastures and hayfields and swamps used for haymaking, also on brackish and even salty soils inside the dykes; moreover on roadsides, along dykes, in light grassy broadleaved forests, in sand dune valleys, in orchards, in peaty marshes and on grassy heaths.

Hubbard, 1954: ... distributed throughout the British Isles in a great variety of habitats, often very abundant; on heaths and moors in hill grassland, old pastures, meadows, and open woodlands; on a wide range of soils from sands to clays; in dry and damp places.

4.2.2 Ecological range in New Zealand

It should not be surprising that observations have been made in New Zealand similar to those made in Europe. As mentioned in Section 3.2, Hooker (1864) stated that it was widely dispersed in New Zealand after about 20 years of colonization by European settlers. Allan (1936) also says that it is "abundantly naturalized throughout and formerly sown to some extent. Plentiful on pastures on light or dry soil that are running out".

Cockayne (1928) mentions A. odoratum as one of the invaders of "low tussock-grassland" (p.213) and that at that time 83 genera of exotic Gramineae had become established in New Zealand (p.354). Only 22 per cent of all the exotics were "very common and common species" which include A. odoratum. This grass, of highly aggressive power elsewhere, is powerless against Danthonia pilosa* (p.363).

Barker (1953) in her study of the tussock grasslands of the Hunters Hills, South Canterbury, finds that A. odoratum is very common in fescue-tussock grasslands where it forms a sward in between the tussocks. Even under grazing it still seeds and spreads. Burning benefits A. odoratum (p.40) which confirms the observations of Strelkova (l.c.) and Dixon (1886). In tall-tussock

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*This species is now probably Notodanthonia pilosa (R.Brown) Zotov, but Mr V.D. Zotov informs me that it could be any or several of the following as well: N. clavata, N. penicillata, N. racemosa, N. gracilis.

grasslands it is not so common but behaves otherwise in very much the same way. In both communities it is most frequent in semi-sheltered localities with eastern aspect.

Moore (1954) described Rumex acetosella communities in the Awatere Valley, Molesworth, Marlborough, where no A. odoratum was found. The vegetation in this area was severely depleted by a very large rabbit population, but now that the rabbits have been drastically reduced in numbers, sweet vernal grass has spread from an area along a stockroute near the Awatere Saddle down to the area described by Moore. It is now widely dispersed throughout Molesworth. This was helped by aerial over-sowing with seed cleanings which contained a large amount of sweet vernal seed (Dr L.B. Moore, pers. comm.).

Connor (1961) records A. odoratum in inland North Otago in Festuca matthewsii communities near Lake Ohau, the Lindis Pass and on the Benmore Range. In many of his relevés it is fairly common, but he has not found it in the Ahuriri Valley. In 1964, Connor published his work on the Mackenzie Country, South Canterbury, and found A. odoratum in fescue-tussock grasslands in very small quantities; it was fairly common in snow-fescue-tussock grasslands especially in the montane zone (about 760 - 1000 metres a.s.l.), and fairly rare in depleted red-tussock grasslands. In the Middle Rakaia Valley, Canterbury, Connor (1965) records A. odoratum in the following communities: snow-tussock grassland: fairly widespread; red-tussock grasslands: fairly widespread; fescue-tussock grassland: common; depleted grassland: common.

It is rather remarkable that A. odoratum is so common in the fescue-tussock grasslands of the Middle Rakaia but nearly absent in those of the Mackenzie Country. It has been suggested that the infrequent

occurrence of sweet vernal in the Mackenzie Country may be due to the extreme drought sometimes experienced in this mountain basin, or to the late frosts which damage panicles and prevent seed setting, or to the previously high rabbit population in this area.

With regards to the first suggestion, it may be that Festuca novae-zelandiae (fescue tussock) is even more drought tolerant in the Mackenzie Country than in the Middle Rakaia; this may explain the different survival of A. odoratum in the fescue-tussock grasslands of these two localities.

Then it may be that late frosts which are common in the New Zealand high country, damage the panicles of sweet vernal and thus prevent seed setting as Hegi (1935, p.277) reports for Central Europe. De Vries (1941a) stresses that A. odoratum suffers badly from severe frosts especially when the soil is waterlogged. In the Mackenzie Country, this may occur during spring thaws, and if this is followed by severe frosts with thin or no snow cover, then the damaging conditions described by de Vries may be experienced. Carroll (1943) also found that A. odoratum was among the grasses most severely injured by low soil temperatures, especially when nitrogen fertilizers had been applied: at $-5^{\circ}C$: 50% survival at low N, 30% at high N; at $-10^{\circ}C$: 20% survival at low N, 10% at high N. He quoted Mail (1940) who observed that a light snow cover of 3/4 to 2 inches (2 to 5 cm) kept the soil temperature at -1° to $-2^{\circ}C$, but in the absence of snow, the soil temperature dropped to $-10^{\circ}C$ at 2 inches when the air temperature was $-13^{\circ}C$.

Finally, it may be that the previously high rabbit population is the cause of the near-absence of A. odoratum in the Mackenzie Country. I have been informed that sweet vernal is now becoming more common in the Mackenzie Country, just as it is in Molesworth (Mr P.T.P. Clifford,

pers. comm.), so that it appears that climatic factors are less important than the biotic factors in this instance of the spread of A. odoratum. Because of practical difficulties no observations and experiments were carried out to test these suggestions.

From unpublished data (N.C. Lambrechtsen) of a snow-tussock grassland survey in the South Island, covering 57 plots of 100 m^2 each and ranging from Porters Pass, Canterbury to Centre Hill, Southland, only 10 plots did not appear to contain any A. odoratum. They were above 1,070 m. in Southland to above 1,300 m. in the Craigieburn Range, Canterbury, and these altitudes roughly correspond with the altitudinal limit observed for A. odoratum.

Further field observations confirm that A. odoratum can be found below a certain altitudinal limit wherever European settlers and their domestic grazing animals have disturbed the native vegetation. It was seen, flowering, on fresh sawdust near a timbermill at Te Kinga, (West Coast); in a very high rainfall area at Sandfly Point near Milford, (South Westland) along a tractor track; in low light conditions along a bush track in Montgomery Park, Banks Peninsula, (Canterbury); at high altitudes about 1,500 m. near Mt Misery, Cass, (Canterbury), in a well grazed, moist valley; on acid pakihi soils in Westland (Mr C.J. Burrows, pers. comm.) and on limestone at Castle Hill, Broken River, (Canterbury). Although there are, no doubt, localities where A. odoratum has not been recorded yet, I firmly believe that it is as widespread as stated above, and that in the hundred years that it has been in New Zealand, it has become established in as wide a range of ecological conditions as observed in Europe.

4.3 REASONS FOR THE ECOLOGICAL ADAPTABILITY

Most of the reasons which aid to explain the ecological adaptability of A. odoratum have been mentioned before, but will be briefly summarized here.

4.3.1 Genetic variability

In his study on the chromosomes of A. odoratum, Jones (1964) stresses the extreme variability in karyotype morphology which may explain the phenotypic polymorphism observed by many botanists. He notes that in Anthoxanthum quadrivalent and even higher multivalent pairing is very common. This provides an opportunity for a high degree of chromosomal and genetic recombination, provided balanced separation of the ancestral sets occurs. Jones suggests that if structural rearrangements of the chromosomes during meiosis are confined to terminal segments and if the pericentric regions which may determine the essential species characteristics thus remain intact, then balanced segregation of the chromosomes will ensure the basic constancy of A. odoratum, while at the same time extensive recombination of terminal segments may produce wide variation in more peripheral characters, e.g. hairiness (see Section 1.5).

Jones's study of the chromosomes confirms Borrill's (1963) findings that A. odoratum is most likely of hybrid origin from A. alpinum x ovatum, which occur in different habitats: A. alpinum in high mountain regions of Europe - Siberia - Japan (see Section 1.3), A. ovatum at sea level and in well-watered mountains in the western Mediterranean region. The former is a winter-hardy perennial while the latter is a variable annual or occasional biennial. A. odoratum can behave both as a perennial and occasionally as an annual which suggests an affinity to both its ancestors as does its ecotypic

flexibility (Borrill l.c.). In my opinion, the work of Borrill and Jones has produced sufficient evidence to support the theory that A. odoratum originated as an allotetraploid hybrid from the diploids A. alpinum and A. ovatum, and that being from ecologically diverse habitats they gave rise to an ecologically adaptable hybrid.

The predominance of cross-fertilization in the out-breeder A. odoratum increases the incidence of rearrangement of genes which leads to further variability and adaptability.

4.3.2 "Weedy characteristics"

Although a weed is usually defined as a plant which grows where one does not want it to grow, it is intended to stress here only those characteristics which enable A. odoratum to grow nearly everywhere as shown in Sections 4.2.1 and 4.2.2. It is not implied that A. odoratum is a weed although many people regard it as such. Most characteristics have been deduced from the description of the life history, Chapter 2.

It has been shown of A. odoratum that:

(a) it has a very large seed production: up to 56,000 seeds per plant (see Section 2.9),

(b) it has awned "seeds" which may bury themselves into suitable sites for establishment more rapidly than de-awned seeds (see Section 2.10),

(c) its seed is viable as soon as it is shed (see Section 2.3), but does not appear to spread very far (see Section 2.10),

(d) its seed remains viable in the soil for many years (see Section 2.11),

(e) its seedling has very low environmental demands.

If sufficient moisture is available, the seed will germinate and grow in almost any light, temperature, and fertility condition (see Section 2.4). The presence of coumarin, an anti-fungal substance, in the seedling, may protect it from some fungal diseases, which might otherwise attack the seedling very successfully (see Section 2.3),

(f) it has very low environmental demands for flowering and seed production. If it has been subjected to night temperatures of less than 5°C for about 10 days and if light and temperature are not too low it will flower and produce seed (see Section 2.9).

From this summary it is clear that seed production and plasticity during development are much greater than necessary to ensure survival and are indeed more probably adapted to give efficient spread after colonization rather than just maintenance. Under these conditions expansion of A. odoratum may occur rapidly until limits are imposed on its further multiplication; the self-adjusting mechanisms of density-dependent mortality and plasticity maintain populations within relatively narrow limits, compared with potential powers of increase (Harper, 1960). He stresses the following points regarding weed populations which apply to A. odoratum populations equally well:

1. A weed population which is at a density such that self-regulation of seed output occurs, will have enormous resilience to change.

2. The seed population bears no direct relationship to the density of weed infestation it will produce; this depends on the frequency with which individual seeds meet microsites suitable for establishment.

3. Responses to density in which plasticity rather than mortality is responsible for population control permit a wider range of genotypes to remain present in the population.

A. odoratum has most of the characteristics of a weed which helps to explain its ecological amplitude.

4.4 AGRICULTURAL ECOLOGY

The agricultural importance of A. odoratum has been considered in Sections 3.1.1 and 3.1.2 from a historical point of view. In this section the behaviour of sweet vernal in pastures will be considered.

The pasture ecologists Kruyne and de Vries (1963) characterized A. odoratum as follows in the Netherlands: "Widespread but not important. It is typical of hayfields with a preference for wet and moist soils. It is rather indifferent to the soil type but prefers more or less acid soils, low in K and P. Not very hardy. Its weight share is much depressed by fertilization with P and Ca, and moderately by N". This ecological description is based on the analysis of more than 1,600 pasture samples taken throughout the country. Others stressed its drought tolerance: Gill and Vear (1958), Strelkova (l.c.), Kirchner et al. (l.c.), Stebler and Schröter (1889) and in New Zealand: Allan (l.c.), see Section 4.2.2. Carroll (1943) studied the drought tolerance of A. odoratum at two nitrogen levels: "high N" and "low N". In a silt loam with a wilting point at 7.7% soil moisture, he obtained the following survival percentages for sweet vernal: at 5% soil moisture: 90% at low N, 80% at high N; at 3% soil moisture: 45% at low N, 30% at high N. Thus Carroll showed that A. odoratum was fairly drought tolerant but not as much as Poa pratensis and Agrostis tenuis which

were some of the other grasses he tested.

Stapledon and his colleagues at the Welsh Plant Breeding Station, Aberystwyth, were very active in the testing of pasture species, including sweet vernal, in the 1920's. It should be kept in mind that in his comparisons with perennial ryegrass and cocksfoot, Stapledon was dealing with virtually unimproved strains; now that greatly improved strains of these two grasses exist, it may well be that his comparisons with the as yet unimproved sweet vernal do not apply any longer.

In 1924, Stapledon found that under a system of frequent cutting (8-10 times a year) sweet vernal compared very favourably with perennial ryegrass. Although the seasonal productivity of perennial ryegrass is not shown by Stapledon (1924) in Figure 4.4.A, the lines give an impression of the performance of single plants of sweet vernal in 1922 which was a fairly dry year, especially in May and June (early summer). This explains the low spring productivity.

Stapledon noted that sweet vernal was as leafy as cocksfoot, tall fescue and tall oat grass, and more so than perennial ryegrass. Hard cutting of sweet vernal reduced yield, tiller number and root weight in the following season. He showed that in a dry year sweet vernal yielded about 60% of the dry matter of perennial ryegrass (50% of that of cocksfoot), but in a wet year it nearly equalled both perennial ryegrass and cocksfoot. When used for hay plus aftermath, sweet vernal produced more than perennial ryegrass.

Under pasture management (imitated by a lawn mower) sweet vernal yielded over a period of 4 years a quarter to half of what perennial ryegrass produced under the same conditions (Stapledon and Davies, 1930). Under hay plus aftermath sweet vernal produced about from half

to more than what perennial ryegrass yielded. The only fertiliser, 6 cwt/ac (6.72 kg/ha) of basic slag, was applied in winter, seven months after sowing. Under a treatment of eight cuttings per annum, it was found that sweet vernal did not respond very much to basic slag; that it was among the highest yielding ones in May (late spring) and that it developed stem shoots (generative shoots) in considerable quantity over a longer period than any other grass.

In a grazing experiment with 12 - 16 weeks old lambs sweet vernal produced more tillers under hard grazing ("four-day rested pasture") than under lax ("monthly rested pasture"); when sown with perennial ryegrass but especially with cocksfoot it benefited also from hard grazing. Cocksfoot does not withstand hard grazing very well. Under lax grazing sweet vernal was suppressed both by perennial ryegrass and cocksfoot (Jones and Jones, 1930).

De Vries (1941b) sampled an old, good quality permanent pasture on heavy clay in the Netherlands and obtained the following figure (Figure 4.4.B) for the percentages by weight of A. odoratum as compared to Lolium perenne during one season. The characteristic high spring and moderate autumn production of sweet vernal stands out clearly in this figure, but its productivity in comparison to perennial ryegrass is low on this type of pasture. However, on a fairly poor, pure hayfield, on peat, De Vries (l.c.) found that sweet vernal contributes up to 18 percent of the total dry herbage sample whereas perennial ryegrass contributes at the most 2 percent.

When fertilized with nitrogen (about 100 kg N/ha per annum) herbage production of sweet vernal was only slightly greater than on the control plot under pasture

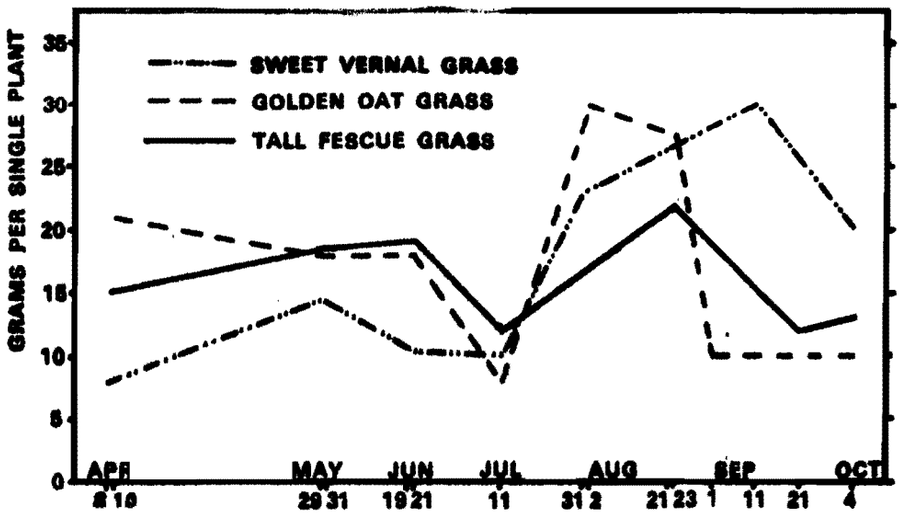


Figure 4.4.A Yield in grams per plant from each of eight 3 weekly cuts. (Figure V, Stapledon, 1924.)

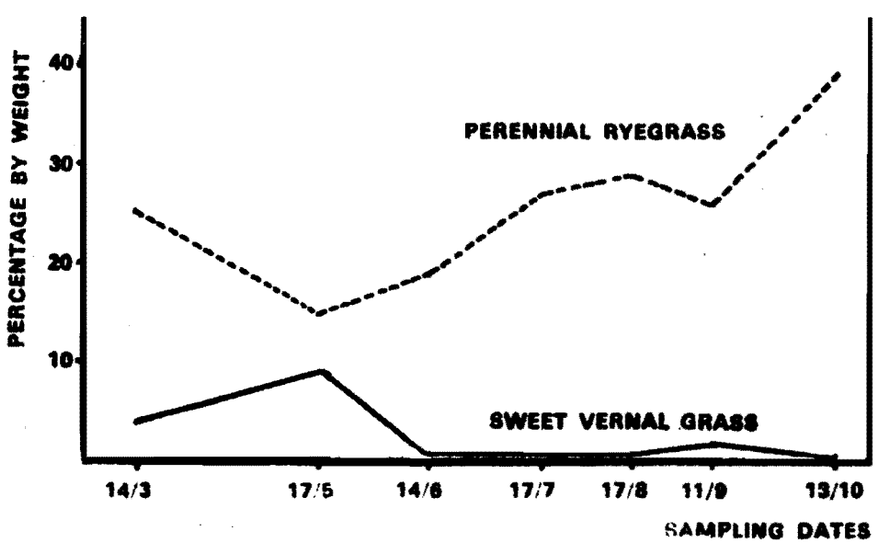


Figure 4.4.B Seasonal percentages of Lolium perenne and Anthoxanthum odoratum in herbage samples from an old, good quality pasture ("Perceel Iwema te Wierum") in the Netherlands. (From Figures 3 and 11, De Vries, 1941b.)

treatment (2 to 9% increase), but under hay treatment the increase was 30 to 40% (Stapledon and Milton, 1932). They also obtained a marked response in tillering to nitrogen (64% increase over control). When sweet vernal was sown on loam, Thomas (1936) found that with a heavy dressing of basic slag and nitrochalk (2,500 kg/ha and 625 kg/ha respectively), sweet vernal produced the highest number of tillers per unit area. Nitro-chalk used with basic slag gave a higher number of tillers per unit area than slag alone, but when nitro-chalk was used alone, the tiller number was no better than on the control plot. This indicates that on this loamy soil, sweet vernal responded better to phosphatic than to nitrogenous fertilizers.

From the results of competition experiments with sweet vernal grass and perennial ryegrass under hay treatment, Davies (1928) classed sweet vernal as: a non-aggressor, but able to withstand some competition in the first harvest year. In subsequent years, it re-established by self-seeding so that even when sown with perennial ryegrass, it produced more in the fourth harvest year than when sown alone. Davies (l.c.) stressed that sweet vernal is not only a profuse self-seeder, but it also flowers early so that it is able to set and shed its seed crop before the normal date of cutting hay. This date usually coincides with anthesis in perennial ryegrass. In the plots without ryegrass, sweet vernal had to compete with unsown plants which had a higher total production over the first four harvest years than sweet vernal itself.

Observations on the palatability of sweet vernal showed that it was grazed by sheep in autumn, winter and early spring but hardly in summer (Davies, 1925). He considered it not very palatable. Similarly, Cockayne

(1920) found in New Zealand that it was readily eaten in spring (September) but neglected in early summer (November).

On a North Island hill country soil at the Grasslands Division hill pasture research area at Te Awa, Suckling (1960) obtained the following yields of sweet vernal growing in small test plots under a heavy fertilizer programme. Other pasture species have been included for comparison.

TABLE 4.4.a Dry matter production in kg/ha. Average for 2 years (from Suckling's Table 1).

	AUTUMN	WINTER	SPRING	SUMMER	TOTAL
Perennial ryegrass	5466	3024	6406	11704	26600
Cocksfoot	5309	1770	6003	8926	22008
Sweet vernal	1568	1792	4122	2296	9778
Yorkshire fog	2016	2453	5992	5331	15792
Browntop	2498	1221	3203	1568	8490

These production figures have been represented graphically in Figure 4.4.C which is based on Suckling's Figures 3 and 4.

Suckling (l.c.) also presented crude protein content data for these pasture species (Table 4.4.b).

It is clear that the average crude protein content of sweet vernal compares very favourably with that of perennial ryegrass and most other pasture grasses shown here. However, it is of more importance whether sweet vernal is grazed readily and as shown above by Davies and by Cockayne, this is only so at certain times of the year.

Suckling (l.c.) placed the above grasses in the following order of annual productivity: perennial ryegrass 100, cocksfoot 83, Yorkshire fog 59, sweet vernal 37 and

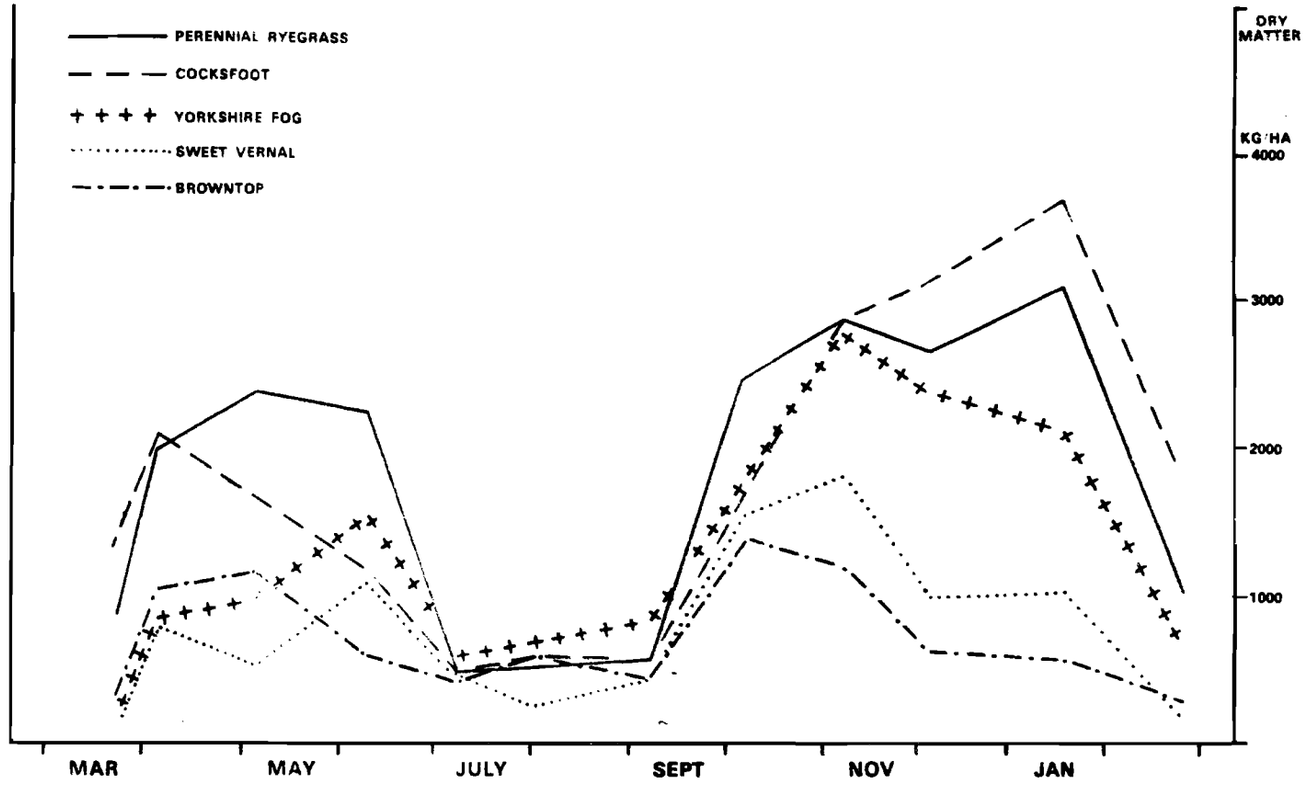


Figure 4.4.C Seasonal productivity of several pasture species in New Zealand. Average for 2 years. (From Figures 3 and 4, Suckling, 1960.)

browntop 32, but again, this does not take grazing preference into account. On the other hand, Suckling's work provides a valuable comparison of the productivity of sweet vernal under New Zealand and European conditions (see De Vries and Stapledon in this Section and also Section 3.1.1).

TABLE 4.4.b Seasonal average crude protein content for the years March 1955 to March 1957 (from Suckling's Table 3)

	AUTUMN	WINTER	SPRING	SUMMER	2 YEAR AVERAGE
Perennial ryegrass	22.5	22.0	15.3	15.4	18.8
Cocksfoot	22.2	26.3	18.5	15.9	20.7
Sweet vernal	21.2	24.2	16.6	15.1	19.3
Yorkshire fog	21.5	22.7	18.1	15.7	19.5
Browntop	22.7	25.8	17.0	16.5	20.5

The response of sweet vernal to fertilizers has recently been studied in New Zealand by O'Connor (1961), Vartha (1963) and O'Connor and Lambrechtsen (1964). On a Craigieburn soil in the Broken River basin, Canterbury, O'Connor (l.c.) obtained a highly significant nitrogen x sulphur interaction for sweet vernal for two seasons. When nitrogen only was applied, browntop yielded more than sweet vernal but with phosphate or sulphur, sweet vernal was superior to browntop in yield. Vartha (l.c.) working on a similar soil along the Ashburton River, Canterbury, found that sweet vernal showed a sulphur response at high nitrogen levels when Yorkshire fog density was low (as in autumn), but when it was high, Yorkshire fog suppressed sweet vernal. Little or no superiority of browntop over sweet vernal in competition for deficient sulphur was

shown; however, when phosphate was applied, the response of sweet vernal was greater than that of browntop and Danthonia species (now Notodanthonia spp.) which confirmed O'Connor's findings. O'Connor and Lambrechtsen (l.c.) carried out burning and fertilizing experiments in snow-tussock grasslands on a colluvial variant of the Dalgety soil near Mackenzie Pass, South Canterbury. Sweet vernal growing in the inter-tussock areas, responded again to applied phosphate, especially on burnt plots. Within the snow-tussocks themselves, there was a marked increase in sweet vernal on fertilized burnt plots, due to both phosphate and sulphur applications. The response to burning observed previously in Section 4.2.2, was confirmed here under experimental conditions.

From the data presented in this Section the following resumé can be drawn up:

1. Sweet vernal was found to be a low to medium producer under pasture treatment and a good producer under hay treatment, when compared to unimproved strains of perennial ryegrass and cocksfoot. (For figures see also Section 3.1.1.) If the same comparison were made now, sweet vernal would be a low producer since it has not been improved as perennial ryegrass and cocksfoot have been.

2. Sweet vernal when by itself responds to nitrogenous fertilizers but on certain soils even more to phosphatic fertilizers. When grown with grasses such as perennial ryegrass and cocksfoot, it is suppressed, although it withstands hard grazing better than cocksfoot.

3. Sweet vernal is grazed to some extent in autumn, winter and early spring depending on the associate grasses and clovers.

4.5 SUMMARY

In this Chapter, it has been shown that *A. odoratum*:

1. is very widespread in both Europe and New Zealand
2. has many "weedy" characteristics which enable it to function as a colonizer
3. is a low yielding grass when compared to improved pasture grasses such as perennial ryegrass and cocksfoot
4. responds to nitrogenous but also to phosphatic fertilizers
5. survives better under hard grazing than under lax grazing because it is suppressed by tall grasses
6. is grazed to some extent in autumn, winter and spring.

CHAPTER 5

PLANT AND ENVIRONMENT

In the previous chapter it has been shown how A. odoratum reacts to various agricultural treatments. In this chapter an attempt will be made to explain these reactions of sweet vernal to its environment by discussing three experiments designed for this purpose.

5.1 INTRODUCTION TO EXPERIMENT A: "SEASONS"

Examples of the effect which environmental conditions have on the development of a plant can be found in any plant physiology textbook. Not only species, but also varieties and even plants within a variety (Troughton, 1965) show distinct reactions to various environmental conditions. The intra-varietal heterogeneity is commonly based on the breeding system of the plant: cross-pollination gives rise to a more diverse collection of genotypes than selfing does. Since A. odoratum is an outbreeder, the heterogeneity is considerable. Mitchell (1953a), to some degree overcame intra-varietal variation by determining the "leaf appearance age" of Lolium plants and related among other variables the rate of tillering to this constant. However, for practical reasons these corrections have not been applied in the present experiments.

In order to investigate the reaction of A. odoratum plants from five localities in New Zealand to different seasonal conditions, growth room studies were carried out at different levels of light and temperature. Unfortunately, insufficient facilities existed at the Botany Department, University of Canterbury, to carry out the experiments simultaneously with plants of the

same age. Professor R.H.M. Langer, Plant Science Department, Lincoln College, University of Canterbury, very kindly made his growth rooms available to me, but the result has been that two growth rooms were used of similar construction (those at Lincoln) and two at the Botany Department, which differed not only from each other but also from those at Lincoln. This may have reduced the significance of the results obtained very considerably. Therefore, the specifications of the four growth rooms have been described in considerable detail in Section 5.2.

Since it had been observed that most growth of sweet vernal takes place in autumn (early winter) and in spring (early summer), these two extremes were chosen. They were combined with sunny and shady conditions since sweet vernal grows in such habitats, so that there were four treatments in this experiment as outlined in the next section. Only the physiological reactions during vegetative development were investigated in this experiment. It was intended that the experiment should establish whether or not ecotypic differentiation had taken place among A. odoratum plants from five localities.

5.2 MATERIAL AND METHODS

Seeds from plants from five localities: Kaikohe (K), Te Awa (TA), Lincoln (L), Gore (G) and Porter's Pass (PP) (for details see Appendix A) were sown on 14 May 1963 on filter paper in petri dishes; on 23 May, when the seedlings were big enough to be handled, they were transferred to pots filled with silver sand and watered with 1N Hoagland solution. From 19 to 21 June, the plants were put singly in 8 cm. diameter plastic pots filled with a homogeneous potting mixture of four parts of soil to three parts of horticultural sand. The

mixture was fertilized with 2.8 kg of dried blood, 1 kg of K_2SO_4, 1.2 kg of superphosphate, 0.8 kg of dolomite and 1 kg of garden-lime per 1 m^3 of soil. If one considers a topsoil of 10 cm depth, the weights of the fertilizers may be regarded as per 10 m^2, or per hectare if multiplied by one thousand.

There were four treatments:

summer-bright (S-B)
summer-dull (S-D)
winter-bright (W-B)
winter-dull (W-D)

The growth rooms or cabinets were situated at:

a) S-B: growth room at Botany Department, University of Canterbury, Christchurch.

b) S-D: growth cabinet at Plant Science Department, Lincoln College, University of Canterbury, Lincoln.

c) W-B: same as for b).

d) W-D: growth cabinet at Botany Department, University of Canterbury, Christchurch.

The specifications are:

Treatment	Light		Light Source in Watts		Temperature in °C	
	Duration in hours	Intensity in f.c.	Fluorescent*	Tungsten	Average	Variation
S-B	12	1420	48 x 80	27 x 15	24	± 1
S-D	12	810	12 x 80	6 x 60	24	16 to 26
W-B	9	1420	18 x 80	6 x 60	10	± 1
W-D	9	810	10 x 40	6 x 60	10	5 to 12

*The fluorescent tubes were ~~WARM~~ WHITE or WARM WHITE tubes

The light intensity was measured in foot candles with a METRAWATT Lightmeter, Type TAVOLUX 2, Ser. No. 3143, with a limit of accuracy of ±5%. All readings were taken at plant level soon after the plants had been put in the growth cabinets. All plants were shielded by glass from the heat of the lamps, except in the growthroom for the S-B treatment at Botany Department. Here, the heat was removed by an airflow directed at the lamps which were 100 to 120 cm above the plants so that the airflow was not noticeable at plant level. There was no humidity control, but all plants were watered daily to ensure optimum growth. The plants were standing in saucers or trays with water to supply moisture through the day.

Twenty pots were used per locality per treatment, but of the Porter's Pass plants only ten plants were available for the S-D treatment and only fifteen for the other treatments. Plants at the same stage of growth were selected to reduce variability. Clones were not used since they might vary as much as seedlings depending on where the tillers were taken from the parent plant (Mitchell and Glenday, 1958). However, the variability found among the seedlings was such that only the average of each measurement has been used for comparison and for statistical treatment.

To avoid differences in the physiological ages of the plants, the pots were put in the growth cabinets at approximately the same time. Unfortunately not all cabinets were available at the same time. The plants that had to wait were kept at low temperatures to retard growth. As is shown below, all plants were acclimatized for about a fortnight, which is ample for readjustment to the climatic conditions in growth cabinets (Mitchell, 1953a). All measurements were carried out at

the same interval where practicable.

Treatment	Date put in growth-cabinet	Measuring dates in number of days after placing in growth-cabinets							Duration of experiment in days
		1	2	3	4	5	6	7	
S-B	24-6-'63	16	22	29	36				23
S-D	15-7-'63	10	18	24	31				24
W-B	15-7-'63	15	22	30	37				24
W-D	26-6-'63	19	25	30	38	44	53	60	44

The following items were measured:

1) Initial and final shoot weight in grammes, both green and dry.

2) Initial and final root weight in grammes, both green and dry.

3) Initial and final tiller number.

4) Leaf blade length in mm on all leaves of the main tiller (symbol 1; for explanation see Section 5.3.3).

5) Ditto on first-leaf tiller (symbol 1.2).

6) "Interblade" length in mm of all leaves on the main tiller and on the first-leaf tiller. This measurement is the length of the sheath between two successive blades.

7) Tiller number on the first-leaf tiller.

8) Sequence of tiller formation on the first-leaf tiller.

On the first measuring date, half of each population was harvested; the plants were selected at random. From these measurements the "initial" data were obtained. On the remaining plants (usually ten) measurements 4 to 8 were carried out, and at the final harvest the "final" data were obtained. For 8, the tillers were tagged with loops of very thin telephone wire of different colours.

5.3 RESULTS

The variability among the plants from each locality obscured the differences between the localities, so that frequently no statistically significant differences could be detected. The use of leaf appearance age as a constant (Mitchell, l.c.) does reduce the intra-varietal variation and suggests that plants of the same physiological age are used, but it involves extra calculations for which the time has not been available. In spite of these reservations, considerable differences in development were found among the localities with respect to seasonal conditions. Frequently plants from the Porter's Pass locality behaved differently from those from the remaining four localities. This suggests that altitude has a greater effect on ecotypic differentiation among A. odoratum plants than latitude.

Since the various treatments were of different durations and since the initial plant weights and sizes differed, growth has been expressed as daily increment, (D.I.), $\frac{W2 - W1}{T2 - T1}$; as relative increment, (R.I.), $\frac{W2 - W1}{W1}$ and sometimes as relative growth rate (R.G.R.), $\frac{\log_e W2 - \log_e W1}{t2 - t1}$, where W1 and W2 are initial and final weight respectively, and t1 and t2 the beginning and the end of the experiment, expressed in days. The suggestion made by Miller (1966) to clarify the terms significant and highly significant, has been applied in the following sections. It is summarized here:

Term	Abbreviation	Conventional meaning
not significant (-ly)	NS	$P \geqslant 0.05$
significant (-ly)	SIG	$0.05 > P \geqslant 0.01$
decisive (-ly)	DEC	$0.01 > P \geqslant 0.001$
conclusive (-ly)	CON	$P < 0.001$

5.3.1 Shoot-root ratios

No significant interactions were obtained among plants from different localities for seasonal conditions for shoot or root dry weight increase although the increase was distinctly higher at S than at W. When expressed as daily increment, there was a trend to a locality x season interaction due to the Porter's Pass plants which had a very much lower increment at W than those from the other four localities. The R.G.R. and R.I. calculations showed that both shoot and root dry weight of Porter's Pass plants increased more rapidly at S and more slowly at W than that of those from the other four localities.

Calculations based on green weight figures showed a significant (nearly decisive) locality x season interaction for shoot D.I., and a decisive locality x season interaction for root R.I. That these interactions were not obtained from the dry weight calculations was probably caused by variations in the dry matter percentages among the plants, this variation being somewhat contrary to the green weight variation. No detailed calculations were made of this dry matter percentage variation.

By combining shoot and root dry weight figures into total plant weight a significant locality x season interaction was obtained for R.I. The analysis of the means shows that plants from the northern localities produce more at W than those from the southern ones which do better at S. This suggests that plants from the north of New Zealand where mild winters are the rule, are less winterdormant than those from the south, which respond more rapidly to mild weather when it arrives after a fairly severe winter. This is particularly striking for the Porter's Pass plants

TABLE 5.3.1.a Analysis of means of relative increase of total plant dry weights

Seasons	Localities						
	K	TA	L	G	PP		
S	6.630	5.138	6.794	7.108	11.108	s.e. = 0.99	L.S.D. 5% = 3.87
W	8.224	5.726	6.540	6.690	4.457		L.S.D. 1% = 6.39
Difference	-1.594	-0.588	0.254	0.418	6.651	s.e. = 1.39	

K = Kaikohe, TA = Te Awa, L = Lincoln, G = Gore, PP = Porter's Pass.

These localities have been described in Appendix A.

from 945 m.a.s.l. which have to be winterdormant in order to survive. The northern plants may be compared to the Mediterranean populations of Lolium and Dactylis studied by Cooper (1963) and the Southern ones to the continental European populations of the same genera.

The figures in Table 5.3.1.a confirm that the latitudinal effect on plant growth is less than the altitudinal effect. No significant interactions were obtained from calculations based on D.I. and R.G.R.

When the R.G.R. and R.I. of the shoot-root ratios (using dry weight figures) were calculated, decisive differences between localities, light intensity and seasonal treatments were obtained, but no inter-actions between these factors. The best root development occurred at W-B, so that the S/R values expressed as R.G.R. and R.I. were mostly negative. The best shoot development occurred at S-D when long, somewhat etiolated leaves were produced and light, brown, fibrous roots. At S-B and W-D, the S/R ratios were not very different although the S-B plants were much healthier looking plants. The decisive locality difference was due to the plants from the Te Awa locality which had a lower S/R ratio than plants from all other localities in all treatments except the summer treatment.

5.3.2 Leaf production and leaf size

The number of leaves produced on the main tiller and the first-leaf tiller was very similar as shown in Figure 5.3.2.A. On the first-leaf tiller slightly less leaves were produced, but the rate was the same as that for the leaves on the main tiller. No statistical analysis has been carried out on the data used for Figure 5.3.2.A. The lines show that a new leaf appears every 7 days under S conditions and once every 8 - 10 days under W. Light

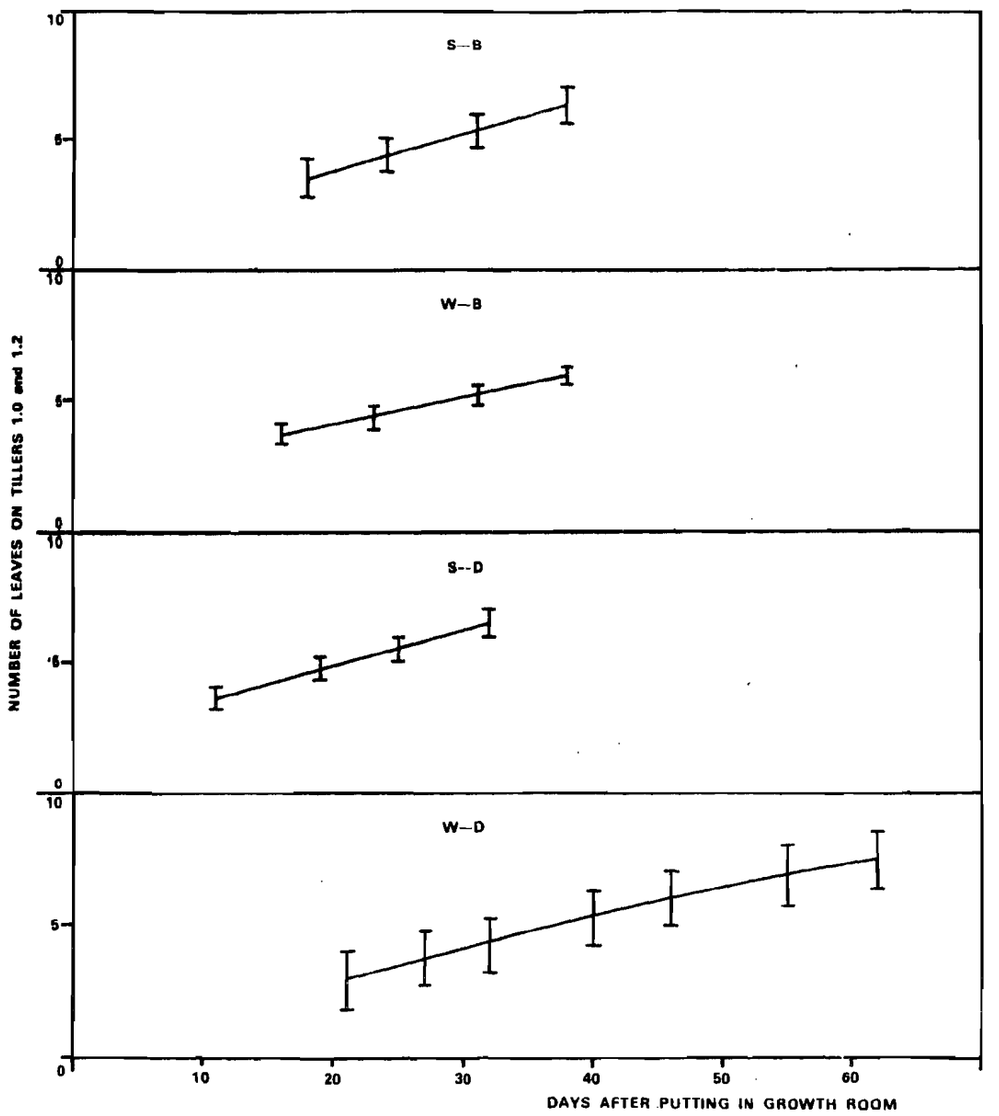


Figure 5.3.2.A Number of leaves per plant under 4 treatments: S-B = Summer - Bright; W-B = Winter - Bright; S-D = Summer - Dull; W-D = Winter - Dull. Vertical bar shows range of locality averages. Part of bar above line approximates values for leaves on tiller 1.0 and that below line for leaves on tiller 1.2.

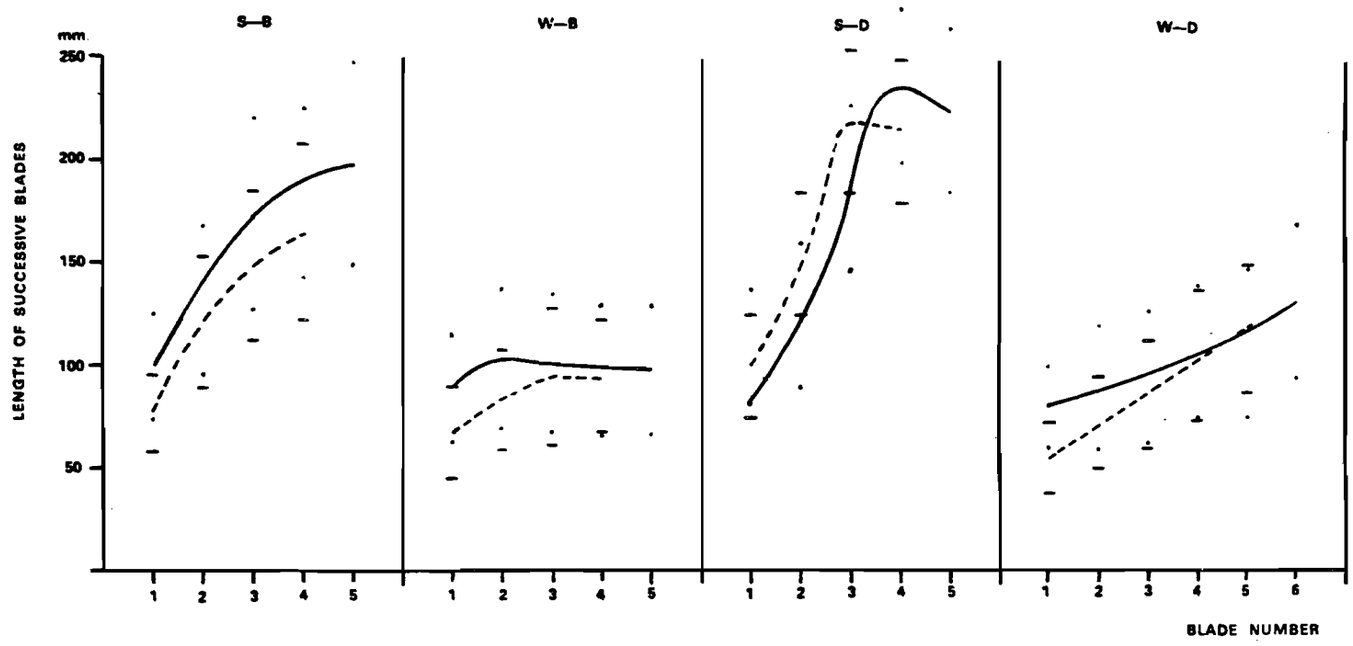


Figure 5.3.2.B Length of successive blades under 4 treatments: S-B = Summer - Bright; W-B = Winter - Bright; S-D = Summer - Dull; W-D = Winter - Dull. Drawn line is average blade length (dots indicate range) of plants from 5 localities on tiller 1.0. Broken line is average blade length (bars indicate range) of plants from 5 localities on tiller 1.2.

intensity has no marked effect on leaf appearance.

The length of successive leaves on the two tillers mentioned before is shown in Figure 5.3.2.B. The leaves of L are nearly always the longest and those of PP the shortest, in all treatments. The leaves on the first-leaf tiller are consistently shorter than those on the main tiller. The longest leaves are produced in S-D conditions and then in decreasing order S-B, W-B, W-D indicating that leaf size is temperature dependent. Optimum leaf-size for plants growing under W-B conditions, is reached very soon; under the remaining conditions the levelling-off of the curves occurs much later. At that stage nutritional stresses or mutual shading may influence leaf size.

The curves for the growth of the third leaf which developed during the period of observation in the various growth-rooms (Figure 5.3.2.C) show a similar sequence for leaf size as noted for Figure 5.3.2.B. Figure 5.3.2.C also shows that leaf elongation stops sooner under bright conditions (after about 15 days) than under dull (after about 20 days) and that the rate of elongation is most rapid at S-D and slowest at W-B.

By combining the results shown in Figures 5.3.2.A and 5.3.2.C it is evident that the rate of leaf appearance is mainly influenced by temperature (as found for Phleum pratense by Langer (1954), and for Lolium by Cooper (1951)), while leaf elongation is mainly influenced by light intensity (as found for wheat by Friend et al. (1962), see Evans et al. (1964). The figures also illustrate that only two leaves are growing at any one time, irrespective of environmental conditions. Langer (l.c.) observed that only 2.0 leaves per tiller were growing on timothy seedlings grown out of doors in late autumn-winter.

TABLE 5.3.2.a Analysis of means of length of third leaf on main tiller

(Lengths in mm)

Seasons	Localities					
	K	TA	L	G	PP	
S	154.3	164.0	224.2	156.6	137.8	s.e. = 8.49 L.S.D. 5% = 23.7
W	113.6	127.8	129.9	102.0	66.0	L.S.D. 1% = 31.2
Difference	40.7	36.2	94.3	54.6	71.8	s.e. = 12.01

TABLE 5.3.2.b Analysis of means of length of third leaf on first-leaf tiller

(Lengths in mm)

Seasons	Localities					
	K	TA	L	G	PP	
S	167.9	166.5	219.4	162.4	150.4	s.e. = 6.59 L.S.D. 5% = 18.4
W	99.5	112.2	109.4	96.4	60.2	L.S.D. 1% = 24.2
Difference	68.4	54.3	110.0	66.0	90.2	s.e. = 9.32

K = Kaikohe, TA = Te Awa, L = Lincoln, G = Gore, PP = Porter's Pass

These localities have been described in Appendix A.

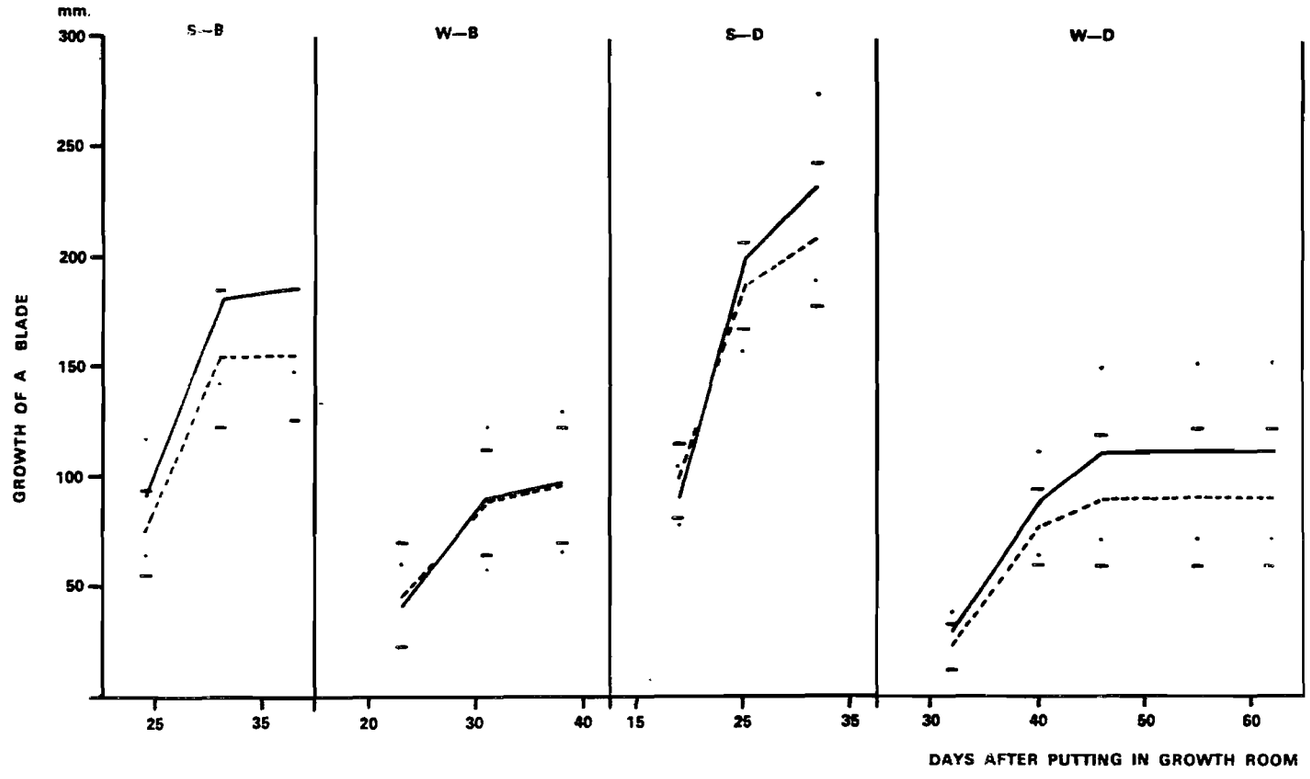


Figure 5.3.2.C Growth of a blade under 4 treatments: S-B = Summer - Bright; W-B = Winter - Bright; S-D = Summer - Dull; W-D = Winter - Dull. Drawn line is average blade length (dots indicate range) of plants from 5 localities on tiller 1.0. Broken line is average blade length (bars indicate range) of plants from 5 localities on tiller 1.2.

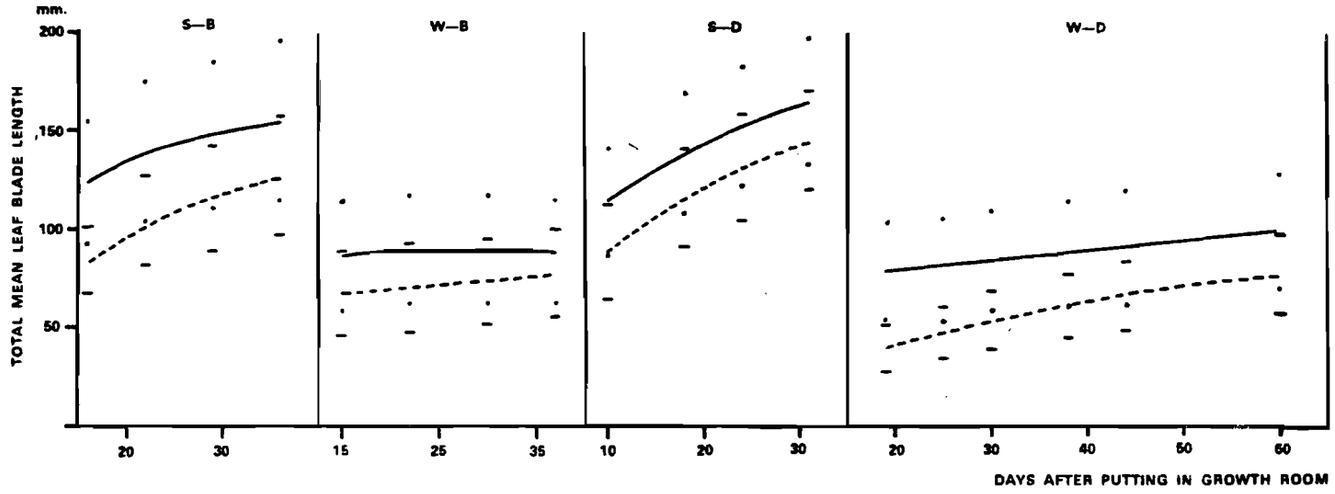


Figure 5.3.2.D Overall mean blade length under 4 treatments: S-B = Summer - Bright; W-B = Winter - Bright; S-D = Summer - Dull; W-D = Winter - Dull. Drawn line is average blade length (dots indicate range) of plants from 5 localities on tiller 1.0. Broken line is average blade length (bars indicate range) of plants from 5 localities on tiller 1.2.

The data used for Figure 5.3.2.C have been analysed statistically; the result was a decisive locality x season interaction on both main tiller and first-leaf tiller. The means are shown in Tables 5.3.2.a and 5.3.2.b.

These data confirm that L produces the longest leaves and PP the shortest in both treatments although under W the leaves of the TA plants are as long as those of L. The differences between the treatments show that leaf growth on TA plants is least affected by low temperatures, whereas that of L and especially of PP is strongly affected. The length of the mean "summer" leaf of PP is 2 to 2½ times that of the "winter" leaf, which points again at its winter dormant behaviour.

From the sum of leaf lengths divided by the number of leaves on that tiller, the average leaf blade length was calculated. This value would have assisted in obtaining total leaf area if the leaf width had been determined. Although this has not been done, it was felt that the average leaf blade length values would give an indication of leaf area since leaf width did not vary greatly among the plants. From statistical calculations on the growth rate of the average leaf blade length on the main tiller a significant difference was found among the localities, caused by the high values for L and the low values for the PP plants. On the first-leaf tiller a decisive locality x season x light intensity interaction was found.

Under summer conditions much larger leaves are produced than under winter conditions, with S-B producing longer leaves among the plants from northern localities and S-D having a similar effect on those from southern localities; the PP plants stand out especially in this respect. This suggests that these plants, being adapted to the high light intensities of montane

environment, can utilize low light more effectively. Under winter conditions PP behaves, with regard to light intensity, as it does under summer conditions (in both cases a ratio of about 4:7), but the northern plants, K and TA, have a higher growth rate in W-D than they have in S-D relative to W-B and S-B respectively. This emphasizes that their winter-active behaviour is most marked in W-D. Under winter conditions, PP has the smallest leaves both in W-B and W-D; this stresses its adaptation to montane environment as mentioned before. The data are presented in Figure 5.3.2.D.

TABLE 5.3.2.C Analysis of means of growth rate of average leaf blade length on first-leaf tiller.

Treatments	Localities					
	K	TA	L	G	PP	
S - B	2.508	1.867	2.626	1.654	1.523	s.e. mean = .1866
S - D	1.915	2.160	2.668	2.534	2.755	L.S.D. 5% = .521
W - B	.670	.412	.706	.662	.424	L.S.D. 1% = .688
W - D	1.107	1.189	1.126	.939	.748	

5.3.3 Tillering

The formation of a shoot from the axillary bud subtended by a leaf, is a process repeated many times during the vegetative development of Gramineae. Since the growing point of most grasses is close to the soil-surface, these axillary shoots or tillers give rise to a tufted plant if they are formed intravaginally, or a spreading plant if they are formed extravaginally. From the buds on the axillary shoot, new tillers may be formed and this process can be repeated several times,

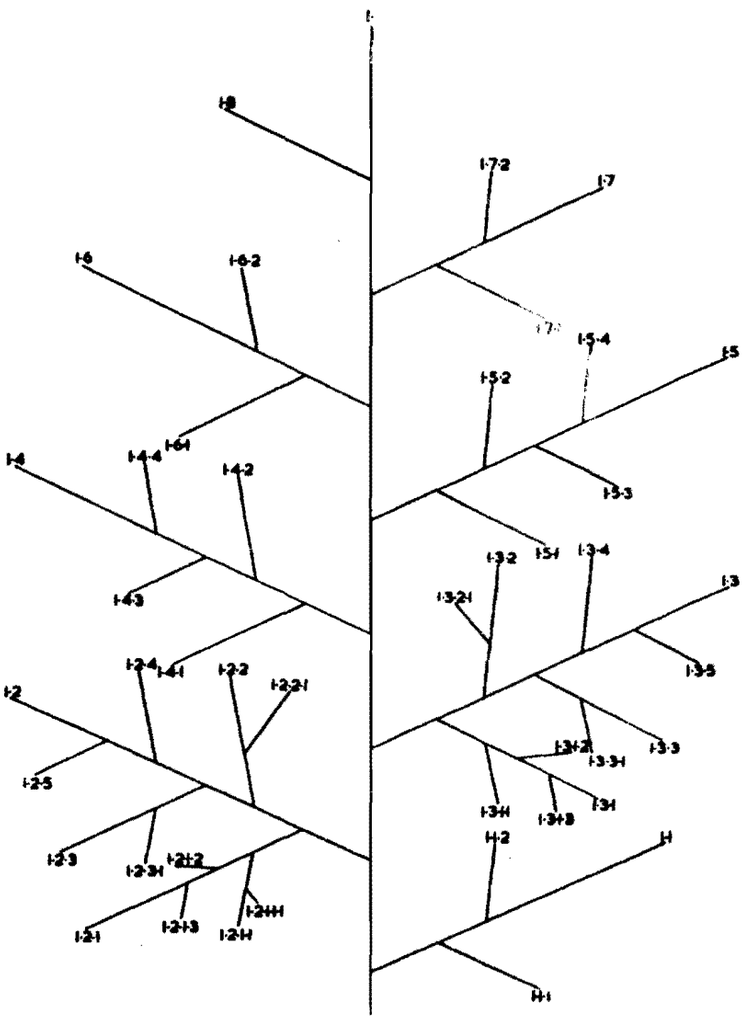


Figure 5.3.3.A Tiller diagram. Each line represents a tiller. Subtending leaves not shown. 1. is the main tiller and 1.2 is the first true leaf tiller.

thus giving rise to a hierarchy of shoots (Langer, 1963). Those on the main stem (symbol 1, sometimes written as 1.0) are usually referred to as primary tillers (symbol 1.1, 1.2, 1.3, etc.), shoots produced by them are secondary tillers (symbol 1.1.1, 1.1.2, etc., 1.2.1, 1.2.2, etc. and so on). The first-leaf tiller mentioned in the previous sections, has symbol 1.2 since the coleoptile tiller is 1.1. Because of the symbols used in this section, primary tillers are also called second degree tillers, secondary tillers now third degree tillers and so on. These symbols were first used by Percival (1921) and later modified by Mr H.E. Connor (pers. comm.). A diagram is shown in Figure 5.3.3.A.

Soon after their appearance, tillers start to form their own adventitious root system, which makes them independent from the parent shoot to some degree. When the vascular connection with the parent shoot is severed, the tiller or tiller clump grows on. This greatly facilitates vegetative propagation. If tillers were to remain vegetative and if no over-crowding were to occur after sometime, the process of tiller- and leaf-formation could carry on indefinitely. Therefore, when studying pasture grasses, it is most necessary to find out which conditions maintain tiller and leaf formation as long as possible, and thus to find out how to obtain maximum leaf production which is maximum yield as far as the agronomist is concerned.

Tiller counts on whole sweet vernal plants were made at the beginning and the end of the experiment; the sequence of tiller formation on the first-leaf tiller (symbol 1.2) was noted at weekly intervals. When the rate of tillering was expressed as daily increment, statistical treatment disclosed a significant locality x season interaction as shown:

TABLE 5.3.3.a \ Analysis of means of daily tiller increment

Seasons	Localities					
	K	TA	L	G	PP	
S	1.121	1.224	.713	1.296	1.451	s.e. = .112
W	1.126	.848	.763	.988	.888	L.S.D. 5% = .311
						L.S.D. 1% = .412
Difference	-.005	.376	-.050	.308	.563	s.e. = .158

The very low rate of tillering of the L plants is offset by its production of large leaves, which supports the concept of a correlation between leaf size and tiller number. It was found that the dry matter production of the L plants did not differ significantly from that of the plants from other localities so that the per tiller production of L is higher than that of the other plants. Since PP has the highest daily tiller increment in the summer season, it has the lowest per tiller production of all localities examined. The higher rate of tillering of PP in the summer is another example of its winterdormant features. Conversely, the K plants (from the northernmost locality) have the highest daily tiller increment in winter, which suggests behaviour similar to the "Mediterranean" plants of Cooper (1963). It is likely that in general, tillering in sweet vernal plants conforms to the pattern observed for pasture grasses: abundant tillering in autumn and spring, but nearly dormant in winter (see Section 2.5). However, when collections of plants from different localities are tested under fairly uniform conditions, physiological differences in the rate of tillering show up; these differences are comparable to those found for total production and leaf growth.

When the rate of tillering on whole plants was expressed as R.G.R. or R.I., no statistically significant differences were found.

In view of the large number of data obtained during the weekly observations on sequence of tiller formation on tiller 1.2, it was decided to illustrate only the tiller pattern of the fourth and fifth order tillers at the end of 24 days when most experiments were terminated. As can be seen from the diagrams in Figures 5.3.3.C and 5.3.3.D, striking differences between localities occurred among tillers in these orders. The diagrams are explained in Figure 5.3.3.B, which folds out. Each quadrant contains a number of classes of tillers formed by a third degree tiller, except in the fourth quadrant where the occasional tiller 1.2.5.1 is also accommodated. The length of each line indicates how frequently the tiller, represented by the line, occurred in ten plants (note the markings in the explanatory diagram).

Figure 5.3.3.C shows the diagrams of tillers of plants from the five localities for S-B (drawn line) and W-D (dotted line). All these plants were of the same physiological age. Under W-D not only fewer classes of tillers were formed per quadrant, but also at a very reduced frequency when compared with S-B. No tillers had been formed in the fourth quadrant and only in plants from two localities was tiller 1.2.3.2 present under W-D. More fifth order tillers had developed under S-B than under W-D. The L plants were the poorest tiller producers under both treatments while PP plants were the best under S-B and K the best under W-D. This fits in with the winterdormant behaviour of the plants from the former and winteractive behaviour of the plants from the latter locality.

In Figure 5.3.3.D the diagrams are shown for the W-B

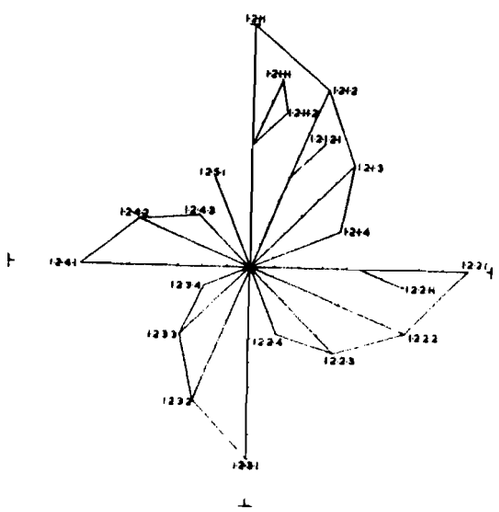


Figure 5.3.3.B Tiller diagram for 4th and 5th order tillers only. Length of each line indicates frequency of occurrence of that tiller on scale 0 - 10. Lines are connected to show size of tiller cluster. Each quadrant contains all tillers formed by a 3rd order tiller, except in the fourth quadrant. This diagram is of the same size as those in Figures 5.3.3.C and D to facilitate comparison.

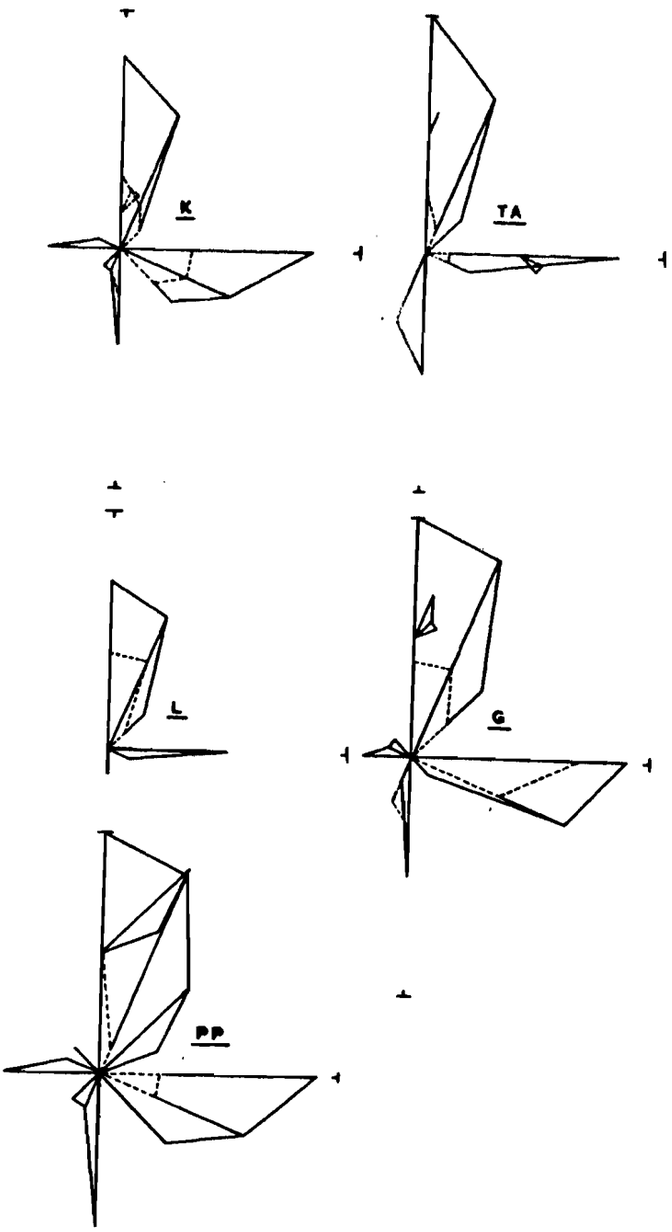


Figure 5.3.3.C 4th and 5th order tillers in plants from 5 localities under 2 treatments: drawn line, S-B (Summer - Bright); broken line, W-D (Winter - Dull). Compare lengths of lines with Figure 5.3.3.B.

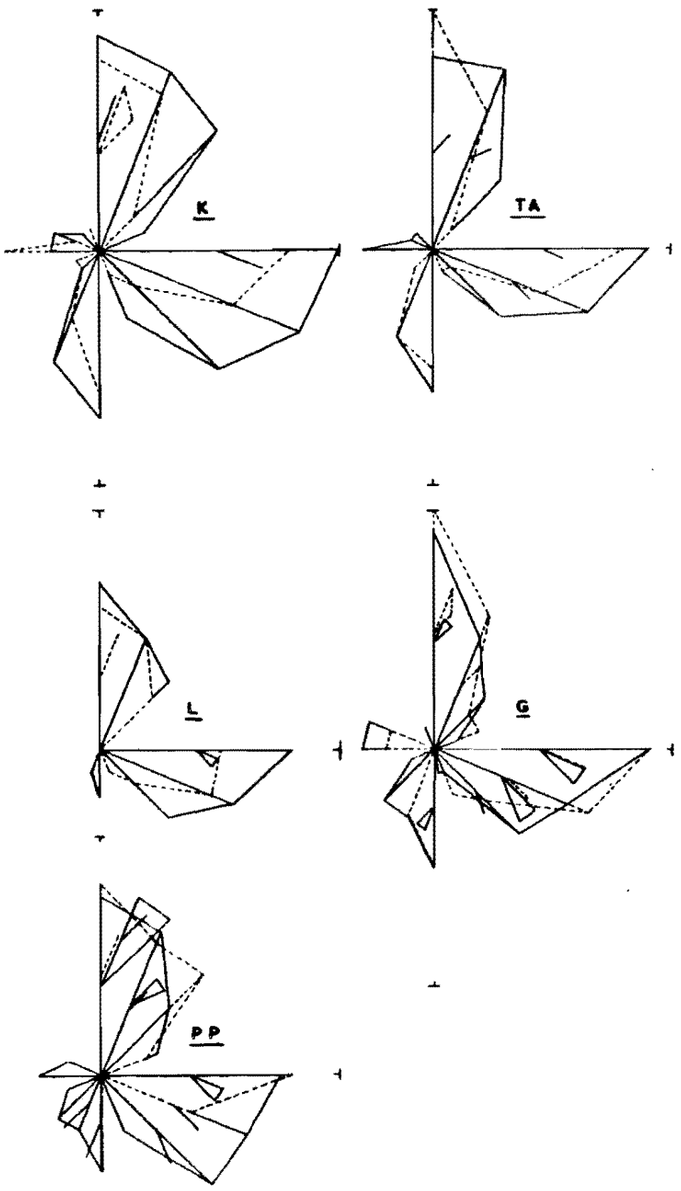


Figure 5.3.3.D 4th and 5th order tillers in plants from 5 localities under 2 treatments: drawn line, W-B (Winter - Bright); broken line, S-D (Summer - Dull). Compare lengths of lines with Figure 5.3.3.B.

(drawn line) and S-D (dotted line) treatments. Again these plants were of the same physiological age, although they were about three weeks older than the plants shown in the previous figure, as pointed out in Section 5.2. At W-B, the K plants had the highest frequency of tillers produced per class, whereas the PP and G plants had the highest number of tiller classes. Thus in different ways, plants may attain the same total tiller number; the figures being 78 tillers for K, 70 for G and 80.5 for PP. In all cases less tillers were produced under S-D than under W-B. It is noticeable that PP, G and to some extent TA have slightly higher frequencies per tiller class under S-D than under W-B. An explanation for this cannot be offered. Under W-B, more fifth order tillers had developed than under S-D. The L plants were again the poorest tiller producers under both treatments.

The diagrams show not only a seasonal difference in tiller formation as observed for the total tiller numbers on the whole plant, but an even more pronounced response to light intensity: under bright conditions not only more tillers per class but also more classes of tillers were formed. Thus A. odoratum requires firstly high light intensity and secondly low temperature for optimum tiller-formation.

Similar observations were made by Mitchell (1953a, b), who found that shading of the meristematic region reduced tiller formation in Lolium species and conversely that with increasing light intensity more tillers were produced, as was also found by Margadant (1950) for Lolium perenne (see review by Langer, 1963). Since A. odoratum is a colonizer of open ground (high light intensity) and also readily suppressed by vigorous grasses in pastures (low light intensity), ecological observations confirm the tiller data from this experiment.

5.3.4 Total interblade length

Measurements of the distance between blades on the main tiller and the first-leaf tiller were taken to get an indication of plant height, which in turn might give an impression of the type of pasture management to which the plants from each locality would be best adapted, low plants being more suited to grazing and tall plants more suited to haymaking.

Statistical analyses of the rate of growth of the total interblade length of plants observed at weekly intervals showed a significant locality x season x light intensity interaction for the measurements taken on the main tiller and a decisive interaction for the same factors for those taken on the first-leaf, as shown in Tables 5.3.4a and b:

TABLE 5.3.4.a Analysis of means of rate of growth of total interblade length on main tiller

Treatments	Localities					
	K	TA	L	G	PP	
S-B	1.189	1.076	1.343	.855	.765	s.e. = .110
S-D	.803	.726	1.037	1.379	.885	L.S.D. 5% = .307
W-B	.533	.400	.584	.533	.400	L.S.D. 1% = .404
W-D	.770	.707	.589	.839	.509	

The data from both tillers illustrate that plants from the northern localities grow taller under S-B than under S-D; the latter induces the plants from southern localities and PP to reach a larger size. Thus, in the summer season there is a positive correlation between plant height and light intensity which is influenced by latitude. However, the PP plants are an exception. One may expect them to benefit from bright conditions which are common at high

altitudes, but instead it shows an inverse relationship: the adaptation to high light intensities in montane environments apparently enables the PP plants to benefit more from low light levels than those of the other populations; in other words it may have higher photosynthetic efficiency.

TABLE 5.3.4.b Analysis of means of rate of growth of total interblade length on first-leaf tiller

Treatments	Localities					
	K	TA	L	G	PP	
S-B	1.439	1.200	1.407	1.015	.703	s.e. = .100
S-D	.790	.761	1.018	1.238	.931	L.S.D. 5% = .278
W-B	.662	.513	.609	.590	.447	L.S.D. 1% = .367
W-D	.748	.714	.676	.815	.490	

In winter, no correlation between plant height and latitude can be observed. The response to light intensity is different: plants from all localities produce the tallest plants under dull conditions. This may be due to etiolation. The PP plants are again the smallest in size of all plants studied, just as they are in S-B. Their small habit may be regarded as another adaptation to montane environment: in winter most foliage gets frosted and in summer high light intensities reduce leaf length and plant size. This makes the PP plants "pasture type" plants while those of the lowland localities are most suited to "haymaking" treatment (see de Vries and Hoogers (1959) in Section 2.5).

5.4 SUMMARY

Although the general validity of the results from this experiment may be doubted because of the differences

in the growth cabinets used for this experiment, it is felt that the following conclusions may be drawn:

(1) Physiologically different behaviour occurs among A. odoratum plants from five localities. The Kaikohe locality contains winteractive plants, whereas the Porter's Pass locality contains winter-dormant plants.

(2) Winteractive behaviour in the Kaikohe (and sometimes in the Te Awa) plants was observed in:

  (a) Relative increase of total plant dry weight

  (b) Growth rate of leaf blade length

  (c) Tiller formation of fourth and fifth degree tillers

  (d) Growth rate of total interblade length.

(3) Winterdormant behaviour in the Porter's Pass plants was observed in:

  (a) Relative increase of total plant dry weight

  (b) Length of third leaf

  (c) Growth rate of leaf blade length

  (d) Daily tiller increment

  (e) Tiller formation of fourth and fifth degree tillers

  (f) Growth rate of total interblade length.

(4) The plants from the remaining localities, Lincoln and Gore, fitted in between these extremes.

(5) The Lincoln plants produced fewer tillers but larger leaves so that the total plant dry weight was still comparable to that of the others.

(6) A. odoratum behaves like other festucoid grasses with respect to rootgrowth, tiller production and rate of leaf appearance although its productivity is low.

5.5 INTRODUCTION TO EXPERIMENT B: "COMPETITION"

It has been observed that A. odoratum is a colonizer of open ground, and that it can persist in low fertility, dry land pastures and in hayfields (see Sections 4.2.1 and 4.2.2). However, as soon as it has to compete with grasses which respond more readily to fertilizers than sweet vernal does, it becomes suppressed and may eventually disappear from a pasture community.

Since sweet vernal is common in the low fertility New Zealand high country it was decided to test its competitive ability against other grasses common in that environment: Agrostis tenuis (browntop) and Holcus lanatus (Yorkshire fog). The growth characteristics of the three grasses used are different: A. tenuis, a short-leaved, densely tillering plant of low habit, H. lanatus, a long-leaved, sparsely tillering plant of tall habit and A. odoratum, an intermediate plant both with respect to leaf length, tillering frequency and habit. By cutting grasses to certain levels, grazing may be simulated and the effect of light on the meristematic region may be ascertained. Under a high cutting system, the mersitematic region would be shaded and in Figures 5.3.3.C and D, it has been shown that tiller production of A. odoratum is strongly reduced in low light conditions. In view of the response of A. odoratum to nitrogenous, phosphatic and sulphatic fertilizers (see Section 4.4), the fertilizer treatments included N, P and S.

Summarising, the following factors affecting growth of A. odoratum were investigated in experiment B:

(1) the presence of other species: A. tenuis and H. lanatus

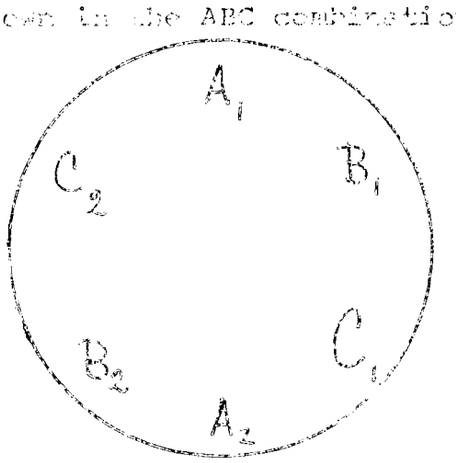
(2) the effect of cutting height

(3) the effect of several fertilizers.

5.C MATERIALS AND METHODS

A. odoratum seed from Department of Agriculture, Gore, and *A. tenuis* (certified New Zealand) and *H. lanatus* seed obtained from a local seed store, was sown on 28.5.84 in boxes and kept in a heated glasshouse. From 27 to 30.7.84 the seedlings, mostly with one or two lateral tillers, were planted in bitumen-painted liver-tins holding 4 kg of moist soil.

The seedlings were planted in a circle with a diameter of 9 cm and 4.5 cm apart (the diameter of the liver-tin was 18 cm). Fejer (1959) states that the spacing of 1½ in. (3.75 cm) between plants is equivalent to that found in a sward, sown at 12 lb/acre = 17 kg/ha., and thus will ensure moderate pasture competition. The following six plant combinations were used: AAA, AAB, AAC, ABB, ABC and ACC where A represented *A. odoratum*, B *A. tenuis*, and C : *H. lanatus*. In this way at least two plants of each species occurred in each tin. They were placed opposite each other as shown in the ABC combination:



The fertilisers had been mixed through the soil before the seedlings were planted in the tins. The potting mixture consisted of four parts of silty loam from Ilam, three parts of horticultural sand and two parts of peat, all sterilized with methyl bromide. This Ilam loam is very infertile : a quick test shows : N as NO_3 : nil; N as NH_4 : low; P : nil; S : very low; pH : 5.5. (For a more detailed soil analysis, see Table 6.1.a.)

Per liver tin the following quantities of fertilizer were added:

N : 3.2 g $Ca(NO_3)_2 .4 H_2O$

P : 1.132 g $CaH_4(PO_4)_2 .H_2O$

S : .613 g $CaSO_4 .2H_2O$.

These amounts may be expressed as 88 kg N/ha, 65 kg P/ha and 27 kg S/ha.

The following fertilizer combinations have been used: $N_0 P_0 S_0$, $N_0 P_0 S_+$, $N_0 P_+ S_0$, $N_0 P_+ S_+$, $N_+ P_0 S_0$, $N_+ P_0 S_+$, $N_+ P_+ S_0$, $N_+ P_+ S_+$; the subscript 0 indicates without and + with the fertilizer added. Although some leaching of the fertilizers did undoubtedly occur, the plant responses obtained have made it clear that this method of fertilizer application was satisfactory when dealing with large quantities of soil.

The cutting treatments were: "high cut" from 15 to 6 cm above soil level; "low cut" from 10 to 3 cm. The plants were cut whenever half of them had reached the required height. Before cutting the plants, all tillers were counted. The cutting dates shown below apply to leaf harvests only.

	"High cut"				"Low cut"				
Counting dates	17/8	1/9	14-15/9	14-16/9	13-17/11	17/8	1/9	23-24/9	7-9/10	5-8/11
Cutting dates			16-17/9	17-20/10	10-12/11			2-3/9	26-29/9	10-12/10	2-4/11

On the last counting dates, the "stubble" was harvested too. This was the length of the plants from 0-6 cm or 0-3 cm. An attempt was made to obtain roots from each pot by washing with a jet of water in a root-washing

installation, but this failed since the peat in the potting mixture was firmly held by the roots.

There were two replicates of each treatment making a total of 192 tins.

The plants were kept at random in a heated glasshouse with average temperatures between 12° and 22°C for a period of three months. No additional light was given. After each counting the tins were re-randomized.

5.7 RESULTS

All results for leaf and stubble harvests are expressed in milligrammes of dry weight. Tiller counts are of all tillers per plant. The dry weight and tiller count data have been analysed separately but a comparison between them will be made at the end of Section 5.7.2.

5.7.1. Leaf and stubble harvests

In the following discussion of the harvests, most attention is focused on A. odoratum as only those data referring to this grass have been analysed statistically. Those of A. tenuis and H. lanatus have been summarized but not analysed, and will only be used where they assist interpretation of the behaviour of A. odoratum.

The results shown in Table 5.7.1.a apply to A. odoratum yields only; they are the means of the average plant weight per tin. To obtain this figure, the totals per tin have been divided by 6, 4 or 2, depending on the plant combination (see Section 5.6).

It is clear from Table 5.7.1.a that A. odoratum tolerates little competition from A. tenuis and even less from H. lanatus; the combination ACC reduces the yield of sweet vernal more than ABB does; similarly AAC has a more pronounced effect on sweet vernal yield than AAB. The combination ABC occupies an intermediate position in the

TABLE 5.7.1.a Mean dryweight in milligrammes per **Anthoxanthum odoratum** plant grown in competition with **Agrostis tenuis and Holcus lanatus**

	LOW CUT TREATMENT							HIGH CUT TREATMENT					
Cutting dates:	2-3/9	26-29/9	10-12/10	2-4/11 Leaf harvests	Total leaf harvests	5-8/11 stubble	GRAND TOTAL	16-17/9	17-20/10	10-12/11 Leaf harvests	Total leaf harvests	13-17/11 stubble	GRAND TOTAL
Plant combinations*													
AAA	88.4	467.2	289.7	348.8	1194.1	675.2	1869.3	223.4	677.2	337.7	1238.3	1326.5	2564.8
AAB	68.4	429.1	225.7	368.3	1091.5	650.7	1742.2	208.5	559.7	255.4	1023.6	1106.6	2130.2
AAC	51.9	404.2	279.8	358.8	1094.7	566.4	1661.1	167.6	316.5	365.6	849.7	1154.0	2003.7
ABB	61.7	392.7	155.4	308.5	918.3	564.2	1482.5	186.9	337.0	275.7	799.6	1159.9	1959.5
ABC	63.8	312.2	311.0	326.7	1013.7	535.6	1549.3	182.9	377.1	223.0	783.0	1076.5	1859.5
ACC	59.9	314.7	250.9	244.5	870.0	419.4	1290.0	200.8	374.8	202.9	778.5	942.5	1721.0
s.e.	5.6	23.5	19.8	36.0		42.1		15.9	35.0	26.1		62.3	
L.S.D. 5%	15.7	66.2	55.9	101.4		118.5		-	98.5	73.4		175.4	
" 1%	20.8	87.7	74.0	134.4		157.2		-	132.6	97.4		232.7	

*see Section 5.6 for explanation.

SUMMARY OF ANALYSIS OF VARIANCE OF EFFECT OF GRASS COMBINATIONS ON GROWTH OF A. odoratum

Combination*													
All A v.mix.	xx	xx	x	-		xx		→x	xx	x		xx	
2A v.1A	-	xx	-	x		xx		-	x	xx		-	
Within 2A	x	-	-	-		-		-	xx	xx		-	
Within 1A	-	-	xx	-		x		-	-	-		-	
NxAll A v. mix.	-	-	-	-		-		-	xx	-		-	

*see Section 5.7.1 for explanation.

high cut treatment, but in the low cut treatment, sweet vernal is less suppressed by ABC than ABB. This is mainly due to the high yield of A in the ABC combination on 10-12 October. The reason for this is not clear since the yields of B and C in the same combination and on the same date were also high.

The plant combinations were statistically analysed as follows using the sweet vernal yield data only:

(a) AAA compared to all other combinations ("all A v. mixtures")

(b) AAB, AAC compared to ABB, ABC, ACC ("2A versus 1A")

(c) AAB compared to AAC ("within 2A")

(d) ABB compared to ABC compared to ACC ("within 1A")

A significant difference may not be obtained when the means within a group of combinations vary considerably. This is the disadvantage of comparing the effect of plant combinations in this manner. However, the same may be said for the comparisons of the fertilizer effect.

The results of the statistical analyses presented in Table 5.7.1.a show that under "low cut" treatment, the yield of sweet vernal leaf and stubble grown in AAA differs decisively from that grown with browntop and Yorkshire fog. The more of the latter grasses are grown with sweet vernal, the less its yield becomes (comparison (b)). Summaries of the yields of browntop and Yorkshire fog (which have not been presented) showed that the total yield of the former was about 12% higher and that of the latter was about 35% higher than that of sweet vernal grown by itself. The results from comparisons (c) and (d) show that regardless of which grass is grown in association with sweet vernal, its yield will be depressed. The only decisive exception is the ABC combination on 10-12 October, mentioned before.

Under "high cut" treatment, the same pattern emerges, but in addition it is clear that it makes a difference whether browntop or Yorkshire fog is grown with sweet vernal (comparison (c)). Yorkshire fog, being a tall plant, suppresses sweet vernal more effectively than browntop which is a short grass (see Section 5.5). When more browntop and Yorkshire fog plants are grown with sweet vernal, no statistically significant effects appear from the analysis of the yield data, but these data do show that Yorkshire fog suppresses sweet vernal more than browntop. From the unpublished summary of the yields of browntop and Yorkshire fog, it was found that browntop produced about 40% more and Yorkshire fog about 65% more than sweet vernal grown by itself, which illustrates that sweet vernal is more easily supressed by tall growing grasses than by low ones. This also supports field evidence that sweet vernal will persist longer in pastures which are kept short. Although its total yield is lower under "low cut" treatment, sweet vernal has a better chance of survival under these conditions than under "high cut" treatment.

From Table 5.7.1.a it is clear that although the total yield of A. odoratum is higher under "high cut" treatment, the total leaf yield is higher under "low cut" treatment. From a grazier's point of view, it is therefore more profitable to graze sweet vernal fairly hard; field observations indicate that it grows best under such treatment and as shown in the previous paragraph, it also has a better chance of withstanding competition from tall plants under "low cut" treatment.

The responses of sweet vernal to fertilizers are shown in Table 5.7.1.b. There is a decisive response to N : first a decrease, then an increase in yield. The responses to P and S are not very clear cut. From a statistical analysis of the yield figures, a decisive P x S interaction has been obtained for the first two

TABLE 5.7.1.b Mean dryweight figures in milligrammes per Anthoxanthum odoratum plant grown at different fertilizer combinations

	LOW CUT TREATMENT							HIGH CUT TREATMENT					
Cutting dates:	2-3/9	26-29/9	10-12/10	2-4/11	Total leaf harvests	5-8/11 stubble	GRAND TOTAL	16-17/9	17-20/10	10-12/11	Total leaf harvests	13-17/11 stubble	GRAND TOTAL
	Leaf harvests							Leaf harvests					
Fertilizer combination* N P S													
0 0 0	71.0	375.2	193.6	183.7	823.5	497.2	1320.7	206.9	254.7	148.2	609.8	1061.5	1671.3
0 0 +	80.8	426.9	193.6	158.1	859.4	517.6	1377.0	207.8	302.2	155.6	665.6	1091.8	1757.4
0 + 0	91.1	430.5	213.8	186.5	921.9	551.1	1473.0	249.8	328.4	163.8	742.0	1051.3	1793.3
0 + +	65.6	342.1	181.2	144.5	733.4	495.7	1229.1	200.1	242.9	137.3	580.3	1028.3	1608.6
+ 0 0	43.5	351.2	312.8	473.1	1180.6	624.2	1804.8	154.9	629.7	457.8	1242.4	1337.8	2580.2
+ 0 +	51.2	363.8	300.2	492.5	1207.7	642.8	1850.5	162.6	564.9	376.2	1103.7	1212.4	2316.1
+ + 0	68.5	430.8	303.5	468.6	1271.4	569.7	1841.1	200.2	582.8	384.8	1167.8	1106.9	2274.7
+ + +	53.8	373.0	318.2	500.5	1245.5	650.3	1895.8	177.9	617.4	389.9	1185.2	1131.5	2316.7

* see Section 5.6 for explanation

SUMMARY OF ANALYSIS OF VARIANCE OF FERTILIZER EFFECT ON HERBAGE PRODUCTION OF A. odoratum

Fert x grasses	-	-	-	-		-		-	x	-		-	
N x grasses	-	-	-	-		-		-	xx	-		-	
N	xx	-	xx	xx		xx		xx	xx	xx		xx	
P x S	xx	xx	-	-		-		-	-	-		-	

leaf harvests under "low cut" treatment. This interaction operates as follows:

at S_0 - P response

at S_+ - P depression

at P_0 - S response

at P_+ - S depression.

At later harvests these responses even out. There is a very small overall P response, an S response at N_0 and an S depression at either N_+ or P_+ and at N_+ P_+ only under "low cut" treatment.

Thus under the conditions prevailing during this experiment, A. odoratum responds very markedly to N but only slightly to P and S. From unpublished data on the associate species A. tenuis and H. lanatus the following observations have been made: for A. tenuis:- a decisive N response, a slight P response and under "low cut" treatment: at N_0 an S response, at N_+ an S depression, both irrespective of P; under "high cut" treatment: generally an S depression except for a response at N_0P_+; for H. lanatus:- a decisive N response, a slight P response and under "low cut" a decisive overall S response; under "high cut": generally an S depression except for a response at N_0P_+.

These findings for A. odoratum agree with its behaviour as described by Kruyne and de Vries (see Section 4.4). They say that the "weight share (of sweet vernal) is much depressed by fertilization with P and Ca, and moderately by N". In other words, it responds fairly well to N, but not very much to P and Ca when compared to other pasture species, which was also found by Stapledon and Milton (see Section 4.4). It is supported by the results from this pot experiment.

The evidence produced from recent experiments with sweet vernal and other high country tussock grassland

species carried out by O'Connor and by Vartha (see Section 4.4) shows some agreement with this pot experiment. The yield of browntop and Yorkshire fog was found to be higher than that of sweet vernal in this experiment regardless of presence or absence of N, P and S, whereas O'Connor found that sweet vernal was superior in yield to browntop when P or S was added in the presence of N. The N x S interaction found for sweet vernal by O'Connor and by Vartha was not observed in this experiment. Only browntop showed an N x S interaction. In this experiment, sweet vernal did not respond to S in the presence of N, but Yorkshire fog did and being a taller plant it suppressed sweet vernal as was observed by O'Connor and by Vartha. In his Table 1, Vartha showed not only the S response of Yorkshire fog, especially at the high N levels, but also the negative N x S interaction obtained for sweet vernal. However, in his discussion he stated that when Yorkshire fog density was low, as in autumn, sweet vernal showed an increasing response to either level (low or high) of S application in the presence of a high level of N application. Possibly because this pot experiment was carried out in spring-summer conditions (and not under autumn conditions when water stress is likely), this response of sweet vernal to S has not been observed. The greater yield response of Yorkshire fog to N when compared to browntop and sweet vernal was also observed by O'Connor who anticipated the possibility of Yorkshire fog dominance under conditions of high fertility when associated with browntop and sweet vernal. The pot experiment discussed here, tends to confirm this. O'Connor's findings that "increase in N supply without concomitant improvement in the supply of S resulted in an almost exclusively browntop harvest" and that "S was not necessary to obtain a browntop yield response from added N in the second year after application" was also confirmed in this experiment:

in the presence of N, browntop yield was markedly depressed by S, especially under the "high cut" treatment.

It is remarkable that browntop, in spite of its low habit, persists well, even under "high cut" treatment, although O'Connor found that sweet vernal tended to become dominant on plots where P and S had been applied in the presence of N. If the present pot experiment had been continued for a longer period, O'Connor's findings might have been confirmed. On the other hand, a neglected, ungrazed or uncut single plant block at Ilam showed browntop dominance over sweet vernal. Ageing single plants of sweet vernal were also invaded and eventually completely dominated by browntop. It appears that after depletion of fertilizers, sweet vernal will ultimately be replaced by browntop in a closed sward because of greater vegetative spread of the latter under moist conditions.

5.7.2. Tiller counts

Prior to each leaf harvest, all tillers per plant were counted on the dates shown in Section 5.6. As it was physically impossible to count and harvest both cutting treatments at the same time, the third, fourth and fifth counting dates did not coincide. However, it was assumed that these dates were sufficiently close together to allow comparison between the "high cut" and the "low cut" treatments, but subsequent checks showed that this could not be done. Therefore, the last counts have been analysed separately and only the first two together. For this reason, the fertilizer interactions in the first two counts are shown in brackets in the lower half of Table 5.7.2.a. The count on 1/9 coincides with the first leaf harvest of the "low cut" treatment, whereas the count on 14-15/9 coincides with the first harvest of the "high cut" treatment. At no stage did the various grass combinations produce a statistically significant effect on tillering

TABLE 5.7.2.a Mean tiller number per *Anthoxanthum odoratum* plant grown in competition with *Agrostis tenuis* and *Holcus lanatus*

	LOW CUT TREATMENT					HIGH CUT TREATMENT				
Counting dates	17/8	1/9	24/9	7-9 /10	5-8 /11	17/8	1/9	14-15/9	14-16/10	13-17/11
Plant combinations										
AAA	4.3	13.3	33.7	38.9	55.4	4.1	11.8	26.6	43.8	52.4
AAB	3.9	12.3	32.1	36.4	56.9	3.9	11.5	23.1	41.1	48.2
AAC	3.8	11.6	31.1	35.6	53.6	4.1	12.2	25.6	40.3	50.6
ABB	3.9	13.3	30.9	34.3	57.3	4.3	12.9	26.4	41.6	52.3
ABC	4.0	12.5	31.4	37.4	52.3	3.9	12.1	24.8	38.6	45.9
ACC	3.8	12.0	33.5	37.2	47.1	4.4	13.0	25.4	38.1	44.3
Fertilizer combination										
O O O	4.0	12.1	29.7	32.6	38.0	4.4	13.9	30.8	40.3	49.4
O O +	4.6	14.7	35.1	36.9	43.5	4.6	13.5	26.8	37.4	47.3
O + O	4.5	14.0	34.1	37.2	44.6	4.3	13.8	28.4	35.2	41.8
O + +	3.8	12.3	31.0	32.6	40.6	4.0	12.3	24.8	32.8	39.6
+ O O	3.5	11.3	32.9	40.4	73.5	4.0	11.1	24.2	50.5	64.3
+ O +	3.4	10.5	28.6	35.0	63.0	3.7	10.4	21.8	41.3	49.6
+ + O	4.1	12.4	34.4	39.5	62.8	4.1	12.9	24.9	45.7	52.6
+ + +	3.8	12.6	31.2	38.8	64.2	4.0	10.0	21.0	41.5	47.0

Symbols for plant and fertilizer combinations have been explained in Section 5.6.

SUMMARY OF ANALYSIS OF VARIANCE OF EFFECT OF FERTILIZERS ON TILLER GROWTH OF *A. odoratum*										
F x G	-	-	-	-	-	-	-	-	-	-
F	-	x	-	-	xx	-	xx	xx	xx	xx
N	x	x	-	x	xx	x	xx	xx	xx	xx
P	-	-	-	-	-	-	-	-	-	xx
S	-	-	-	-	-	-	x	xx	x	x
NP	(x)*	(x)	-	-	-	(x)	(x)	-	-	-
NS	-	(x)	-	-	-	-	(x)	-	-	-
PS	-	-	-	-	-	-	(x)	-	-	-
NPS	-	-	-	x	x	(x)	-	-	-	-

*The interactions on the first two counting dates have been bracketed to indicate that the fertilizer effects in the two cutting treatments were analysed together.

of A. odoratum.

The results presented in Table 5.7.2.a show that fertilizers, especially N, had a significant effect on tillering of A. odoratum. In the first three counts, N depressed tiller formation (equilibrium was reached in "low cut" at the third count) and then increased tiller formation. Sulphur consistently depressed tiller formation in the "high cut" treatment, but only slightly so in the "low cut" treatment. In the final "high cut" count, P depressed tiller formation. No decisive fertilizer interactions were observed. Nitrogen is thus the only fertilizer which markedly affects tiller formation in A. odoratum; when the quantity of N is high, it suppresses tiller formation; when it is low as at the final counts, it increases tiller formation. No striking differences between the cutting treatments were found; the tiller number tended to be higher under the "low cut" treatment than under the "high cut". This suggests that A. odoratum requires light for tiller formation although in a very moderate degree. Most grasses require light for tiller formation (Langer, 1963). Under "low cut" or short pasture conditions, sweet vernal will thus form more tillers and since its tillers do not spread, it will form a caespitose plant. This is confirmed by de Vries and Hoogers (1959) who found that A. odoratum was less tufted in "pure hayfields" than in "pure pastures" (see also Section 2.5).

The competition experiment carried out by Van den Bergh and de Wit (1960) who used A. odoratum and Phleum pratense, showed that the "relative reproductive rates" (based on tiller counts) of these two grasses grown under constant environmental conditions was independent of the relative frequency of the species. These findings tend to support my conclusion that tiller production of A. odoratum is not seriously affected by certain associate

grasses. However, it is unfortunate that Van den Bergh and de Wit discarded the herbage each time they cut the plants from 20 cm to 4 cm. If they had kept and weighed the herbage, they might have found a significant difference between the "reproductive rates" of these two grasses. Obviously, I do not agree with their statement that tiller number is a useful factor to explain competition among plants. When used in conjunction with herbage yield data, tiller numbers may assist in explaining competition.

Van den Bergh and Elberse (1962) carried out another competition experiment along the lines developed by de Wit; this time they used A. odoratum and Lolium perenne. From the "relative reproductive rates" they showed that at low P and K, A. odoratum will drive out L. perenne, but at high P and K, the reverse is the case. After three months they observed symptoms which were attributed to a virus; they assumed that sweet vernal might be a carrier of a host of viruses as well as being a symptomless carrier of yellow-dwarf virus. They discounted the possibility that coumarin excreted from the roots of A. odoratum caused these virus symptoms and as will be shown in Chapter 8, coumarin is unlikely to play a role in competition.

Recent work by Catherall (1966a) shows that virus diseases may have a very significant effect on the productivity of Dactylis glomerata and Lolium perenne. Cocksfoot streak virus was found to affect horizontal growth, whereas barley yellow dwarf virus affected vertical growth; this in turn was found to affect the competitive ability of these two grasses. Although it is not known to what extent A. tenuis and H. lanatus, used in the present experiment, are affected by viruses, yet another virus has been found in A. odoratum (Catherall, 1966b), and it may well be that viruses play an important role in the competition of A. odoratum with other plants, particularly grasses.

5.8 CONCLUSION AND SUMMARY

The data from this experiment may be analysed in a different way at some future date in order to obtain a more precise understanding of the mechanisms underlying competition of A. odoratum with other grasses, but for the present time, it is felt that the following conclusions may be made.

Herbage production and tiller formation of A. odoratum are affected in a similar manner by fertilizers especially N, but the effect of associate grasses is only shown in its herbage production and not in its tiller formation. This means that if A. odoratum is suppressed by more vigorous grasses for a period of two to three months, it will still produce enough tillers which can form leaves to fill the space in the canopy left by other grasses when they become less vigorous. At the end of this experiment, when most fertilizers had been depleted, A. odoratum appeared to be able to utilize better what was left of the fertilizers than A. tenuis and H. lanatus. In a stand of vegetation where these three grasses are common, A. odoratum tends to become dominant when P and S have been applied in the presence of N as found by O'Connor (see Section 5.7.1). However, when A. odoratum continues to be suppressed by more vigorous grasses, it will disappear as mentioned by Kirchner, Loew and Schröter (see Section 4.1). Low light near the meristematic region of A. odoratum may be the primary reason for its disappearance from a plant community. How this low light is brought about is immaterial but it will have to be for a prolonged period to be effective, since A. odoratum has been found to grow at forest margins and along forest tracks where light near its meristematic region may be even lower than in a dense, tall pasture. No experiments have been carried out to

test this hypothesis, although the decisive reduction in tiller production of A. odoratum under low light conditions has been illustrated in Figures 5.3.3.C and D.

The responses of A. odoratum to fertilizers, especially N, are approximately the same, whether expressed as herbage yield or as tiller number: first N depression, then N response. The P and S fertilizers do not have a marked effect on sweet vernal, although as suggested in the previous paragraph, under low fertility conditions A. odoratum may utilize what fertility is left, more efficiently than its associate grasses in this experiment. Whether this could be explained by the low cation exchange capacity of sweet vernal roots, I am not prepared to say. That the "weight share of sweet vernal is much depressed by fertilization with P ....." as found by Kruyne and de Vries is confirmed by the low P response of this grass in this pot experiment.

The results for A. odoratum from this competition experiment may be summarized as follows:

(1) its tiller production is not affected by the two associate grasses, Agrostis tenuis and Holcus lanatus, over a period of three months,

(2) its herbage production is reduced by A. tenuis and even more so by H. lanatus; under the "high cut" treatment the effect is more pronounced than under "low cut",

(3) its tiller and its herbage production is affected in approximately the same manner by fertilizers, mainly N: first N depression, then N response; its response to P is low; S depressed tiller number under "high cut" treatment, tended to do so under "low cut", and did not affect herbage production.

5.9 INTRODUCTION TO EXPERIMENT C : "HIGH ALTITUDE EXPERIMENTS"

Because of the importance of A. odoratum in the New Zealand high country as a colonizer and as a supplier of spring feed, experiments were carried out in two localities to establish the altitudinal limit of this grass and some of the factors affecting this limit. The first area was in the Craigieburn Range, Canterbury, and the second in the Black Birch Range, Marlborough.

5.9.1. Craigieburn experiments

A. odoratum plants were taken on 15 February 1963 from Dry Creek, a montane locality near Porter's Pass (see Appendix A for site description) and were established at 1220 m and 1584 m a.s.l. along the Canterbury Winter Sports Club ski-road leading to Mt Cockayne, Craigieburn Range, Canterbury, on 25 March 1963 (see Appendix A for description of experimental sites). All ten plants were put singly in livertins (similar to the ones used in Experiment B, (see Section 5.6) which had been filled with a good potting mixture so that survival was determined mainly by climatic and not edaphic factors.

The 1220 m site was on a bare eroded slope of exposed subsoil, aspect NE, slope 22°. Five plants were put in this site which was fenced off to exclude sheep, but not deer, rabbits, grasshoppers and other grazing animals. The tins were embedded firmly into the subsoil to prevent movement downhill. Subsequent inspections showed that although the tins remained firmly embedded, the protective stones and boulders surrounding the tins had moved at least six inches downhill during the winter and the following spring (see Figures 5.9.1.A, B).

At the 1585 m site, which is well above the local altitudinal limit of about 1300 m for A. odoratum, the

remaining five plants were established in alpine tussock grasslands, aspect E N E, slope 16°. On 22 November 1963 a wire-netting cage was put over these plants to exclude all large grazing animals; grasshoppers, field mice and other small herbivores still had access to the plants. They survived only for one, possibly two winters at this altitude. Therefore plants grown from Norwegian seed were put in this site under a wire netting cage on 22 March 1964, but of the initial nineteen plants only five were still alive after one winter and only three after two winters. The seed was labelled A. alpinum. This species occurs at high altitudes in Europe and is regarded by some taxonomists as a diploid form of A. odoratum, since these two species are morphologically very similar. However, for reasons outlined in Section 1.5, I consider A. alpinum to be a true species.

Table 5.9.1.a shows that all plants survived at the 1220 m site in spite of the severity of the environment. No meteorological observations have been carried out at this site, but detailed climatological investigations are being made in the adjoining valley by the New Zealand Forest Service. Some results have been published by Morris (1965). His station "Alans", AO, appears to be somewhat similar to the 1220 m site and his "Ski Basin", SB, to the 1585 m site. Therefore some of his observations and conclusions have been used during the discussion of the performance of sweet vernal plants at my two sites. My own observations suggest that considerable temperature fluctuations occur on and in the exposed subsoil slope at the 1220 m site, which give rise to frost-heave when the soil is sufficiently moist; this could explain the large scale movement of rocks and other debris. Some short-term solifluction may assist this movement of rocks and other debris. This site is also exposed to frequent, strong N W winds which deposit dust and other small soil

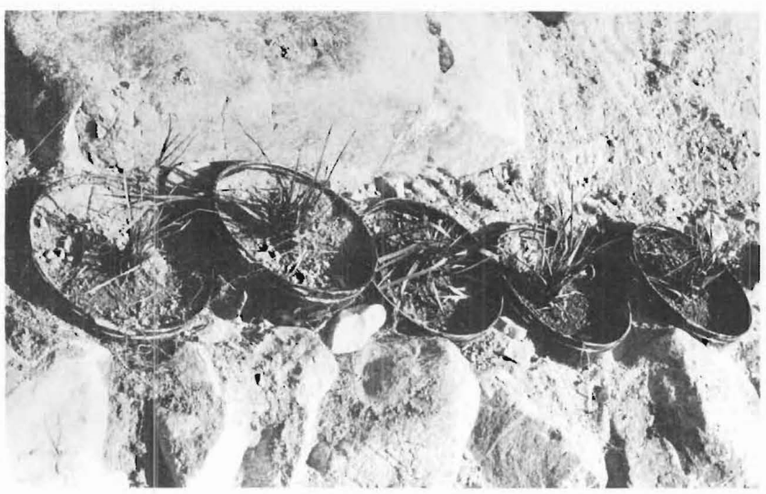


Figure 5.9.1.A Plants at Craigieburn Mountains, 1220 m. site. (Photo taken 25-3-1963.)

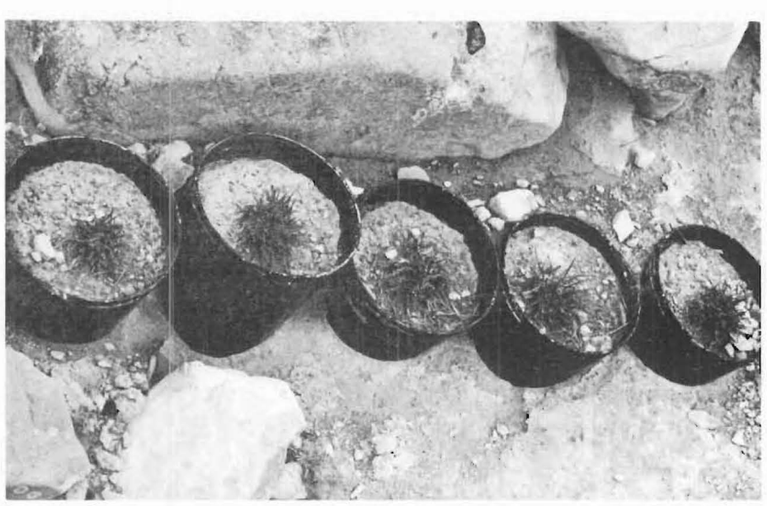


Figure 5.9.1.B Plants at Craigieburn Mountains, 1220 m. site. Note downhill movement of stones in one winter. (Photo taken 25-10-1963.)

TABLE 5.9.1.a Growth of A. odoratum plants at Craigieburn Mountains, Canterbury

Site A at 1220 m a.s.l.

Planted 25 March, 1963

Measurements in cm.

Plant	Inspection dates	Tiller No.	Culm No.	Culm length	Panicle length	Av. leaf length	Av. leaf width	Plant height
1	25.10.63	44	10			2	0.4	*
	22.11.63	53				2	0.4	*
	5. 2.64	56	35	10		4	0.4	3
	22. 3.64	70	32	12		4	0.45	6
	18. 1.65	47	31	6		4	0.4	4
	17. 4.65	60	31	13		3.5	0.45	3
	5. 1.66	70	35	10	1.5	2.5	0.4	1.5
2		100	1			3	0.35	*
		105				3.5	0.4	*
		100+	56	13		3	0.4	4
	See above	100+	44	11		3	0.35	5
		90	14	15		7	0.35	5
		110	20	15	2.5	6	0.4	5
		100	30	11	2	3	0.3	2.5
3		75	5			1.5	0.4	*
		80				3	0.4	*
		60	41	15		4	0.35	4
	See above	80	56	17		3.5	0.5	6
		60	36	15		4	0.4	5
		70	27	15		4	0.4	5
		60	32	6	1.5	2.5	0.4	2
4		55				2.5	0.4	*
		63				3	0.45	*
		60	27	18		4	0.4	5
	See above	60	38	19		5	0.5	7
		50	12	5		6	0.5	4
		70	8	14	2	5	0.45	4
		50	10	6	1.5	3	0.4	3
5		43	17			2	0.35	*
		51				3	0.4	*
		50	37	10		3	0.4	5
	See above	40	18	18		4	0.45	5
		31	15	6		3.5	0.45	4
		45	20	10		3	0.4	3
		50	12	4.5	1.0	2	0.4	1.5

*See leaf length

particles on sheltered slopes and in existing vegetation (Molloy, 1963). Such deposits have been found among the five sweet vernal plants; they may explain how this grass can appear to be a geophyte as observed by Gams in the European Alps (quoted by Strelkova, see Section 2.5).

From Table 5.9.1.a it is clear that soon after their establishment the plants reached a certain size (as expressed by tiller number) which then remained fairly constant, new tillers were formed and old ones died. The plants formed panicles in January-February and in March "seed" which looked viable was found in a panicle. Viable "seed" was observed only once because the "seed" would be blown away as soon as it was ready for shedding. In spite of this single observation, I am of the opinion that sweet vernal regularly completes its life cycle at this altitude although it flowers very late (at Ilam, flowering takes place from the middle of October onwards, see Section 2.7) and although the green panicles are removed by grazing animals and strong winds. Both Morris (l.c.) and Molloy (l.c.) find that January and February are the only relatively frost-free months at this altitude and therefore A. odoratum can only successfully produce panicles in these months. Earlier frosts cause the panicles to shrivel up (see Section 4.2.2). Morris stresses the shortness of the frost-free season and the growing season which is "why attention is being focussed on the introduction of plants with a growing season short enough to allow them to escape some of this damage". Since sweet vernal can keep on producing new panicles (Section 2.6.1) when earlier ones have shrivelled up, and since its "seed" is formed and ripened quickly, it can complete its reproductive cycle within the frost-free period at the 1220 m site. However, no seedlings were observed in the trial site. This was probably caused by the lack of soil

cover which created conditions adverse to plant establishment: soil instability, large fluctuations in temperature and soil moisture. Furthermore, the low fertility of the subsoil did not encourage plant establishment.

The culm length and panicle length data in Table 5.9.1.a compare well with measurements carried out on sweet vernal populations from other montane localities. Grazing in the early stages of panicle development may explain the very small size of the panicles on 5-1-'66. Leaf length and width did not vary greatly over the period of observation although leaf length is affected by grazing. This is severe soon after the disappearance of snow in spring and tends to become less severe from the middle of January onwards. The "plant height" figures which are of vegetative height of the plant only, support the observations made on leaf length. The grazing pattern may be due in part to the low coumarin levels of sweet vernal leaves during the early stages of development (see Chapter 8) and in part to the scarcity of food after the disappearance of snow.

Table 5.9.1.b shows that no plants survived more than two winters at the 1585 m site. If the observation made on 18-1-'65 is correct:- 'the plants had been dead for a long time and might not have survived the autumn of 1964', then the plants lasted for one winter only. Even if they had survived at this altitude, the panicles they formed were either grazed when the plants were not yet protected by a cage or were sterile due to frost damage. Morris (l.c.) shows that the normal frost-free period at his S.B. station is only 25-29 days and this is obviously too short to enable sweet vernal to form panicles and to set "seed".

The A. alpinum plants established at the 1585 m site did not survive much better in this environment; only three plants were alive after two winters and although culms were seen, the panicles had been chewed off by small

TABLE 5.9.1.b Growth of A. odoratum and A. alpinum plants at Craigieburn Mountains, Canterbury

Site B at 1585 m a.s.l.

A. odoratum planted 25 March, 1963.

A. alpinum planted 22 March, 1964.

Measurements in cm

Plant No.	Inspection dates	Tiller No.	Culm No.	Culm Length	Av. leaf length	Av. leaf width	Plant height
1	25.10.63	† (dead)					
	22.11.63	†					
	5. 2.64	†					
	22. 3.64	†					
(2)	18. 1.65	† (42)			(up to 3)	(0.3)	(up to 4)
	17. 4.65	† (75)				(0.3)	(1)
	5. 1.66	† (80)			(up to 3)	(0.3)	(1.5)
2		10			3	0.4	*
		13			1.5	0.4	*
	see	12			2.5	0.4	*
	above	21	3	up to 17	4	0.55	8
(3)		† (68)			(2)	(0.3)	(up to 4)
		† (85)				(0.3)	(1)
		† (95)			(up to 2)	(0.3)	(1)
3		11			4.5	0.4	*
		15			3.5	0.35	*
		24	5		5	0.4	*
	see above	9			5.5	0.5	5
(4)		† (11)			(2)	(0.3)	(up to 4)
		† (50)				(0.3)	(1)
		† (25)			(1)	(0.3)	(0.5)
4		11			3.5	0.4	*
		18			3	0.45	*
		30	10		6	0.5	*
	see	28	6	up to 14	5.5	0.5	9
(7)	above	† (19)			(up to 3)	(0.3)	(up to 4)
		† (†)					
		† (†)					
5		9			3	0.45	*
		8			1.5	0.35	*
		†					
		†					
(9)		† (3)			(2)	(0.3)	(up to 4)
		† (†)					
		† (†)					

*See leaf length

Note: All figures in brackets refer to A. alpinum plants.

herbivores. The plant height and leaf length data show that these plants are subjected to severe grazing. Many dead leaves were found to surround the tillers on 17-4-'65. They might protect the meristematic regions and ensure survival of the tillers (see observation on 5-1-'66) although they had been grazed very short. It seems unlikely to me that even the A. alpinum plants will survive at this altitude although the site is more sheltered from strong winds than the lower site.

The conclusions from this experiment are:

A (1) At 1220 m, which is below the local altitudinal limit of about 1300 m, A. odoratum completes its life cycle although seedlings were not observed in the experimental site. The plants do not expand in size every year.

A (2) At this altitude, A. odoratum flowers in January and sets seed in February, the only relatively frost-free months. Panicles may be removed by grazing animals or strong winds.

B (1) At 1585 m, A. odoratum dies after one to two years and even A. alpinum may not survive for many years. No seed-forming panicles are produced.

B (2) The death of A. odoratum may be attributed to any or a combination of the following factors: frequent occurrence of frosts; shortness of the growing season; grazing by small herbivores; the occurrence of spring droughts (see Morris, l.c.).

5.9.2. Black Birch experiment

This experiment was part of a project (No.6213) designed by Dr K.F. O'Connor, Grasslands Division, D.S.I.R., to evaluate the ability of several grasses to

survive and grow in Notodanthonia setifolia grassland under different fertility conditions and also to evaluate their ability to withstand frost heaving. Among the twenty lines of grasses investigated were A. odoratum plants from the lowland localities: Kaikohe, Te Awa, Lincoln and Gore. Some of the results have already been published, see O'Connor and Lambrechtsen (1967).

The grasses were established on the Black Birch Range (Marlborough) near the temporary Black Birch Observatory (41°45'S, 173°48'E) at 1370 m in a trial area surrounded by a rabbit and deer-proof fence on an E slope of 2-3°. The soil is very low in N and available P. For additional data see O'Connor and Lambrechtsen (l.c.). Detailed climatological observations have been presented by Bateson (1964). They have been summarized by O'Connor and Lambrechtsen (l.c.) and Coulter (1967). The climate at this site is characterized by frequent, strong N W winds, fog, snow, hail, frost in every month of the year, evenly distributed annual rainfall of 138 cm, moderate maximum temperatures (up to 22°C) and moderate frosts (down to -9.5°C). In spite of frequent fogs (up to 22 days per month), high readings for bright sunshine were obtained : annual total, 2141 hours; highest monthly reading, 268 hours in January. For more details see Coulter (l.c.).

The trial was laid out on exposed subsoil in nine plots. There were three fertilizer treatments: NIL, P at 1000 kg of superphosphate per ha and N + P at 112 kg N per ha as urea and the same amount of superphosphate as before. The treatments were repeated three times. The twenty lines of grasses were planted as to 4 - 10 tillered clumps on 31-10-'62, each line being represented by five plants per plot, and oversown with inoculated white clover seed at 4.5 kg per ha. On the same day the fertilizers were put on.

Visits to the site were made on 24-4-'63, 18-9-'63, 3-6-'64, 28-10-'64, and 5-4-'66. During the first inspection, observations were made only on the no-fertilizer plots, but at subsequent visits all plots were examined as the plants on the NIL plots were nearly all dead. On 28-10-'64 heaved out plants were replaced and fertilizers applied at a rate approximately ¼ of the initial dressings.

Observations were made on the following: leaf length, leaf width, tiller number, culm number and culm length. Notes were made on the degree of frost-heaving; this was frequently so considerable that plants appeared to have moved downslope within their rows, although the area was approximately flat. The rows followed the direction of the slope. Table 5.9.2.a presents the results of the heave scores. Per fertilizer treatment fifteen plants from each locality were planted. The "heaved" plants included both completely and partly heaved out plants; the latter were sometimes still alive. This explains why in two cases the number of plants scored after the second winter is higher than the number of "not-heaved" plants after the first winter. The "not-heaved" plants represent some of the survivors. Direct comparison of this Table with Table 3 of O'Connor and Lambrechtsen (l.c.) is thus not possible.

The "1st winter" observations were made on 18-9-'63 and those for the "2nd winter" on 28-10-'64.

Table 5.9.2.a shows that without fertilizers very few plants survived two winters, only a few plants from the South Island localities stayed alive. With P only, there was still considerable frost-heave damage although most plants not heaved in the first winter survived the second winter. With N + P added, little damage was done to the plants and again most plants not heaved in the first winter survived the second winter, with the exception

TABLE 5.9.2.a Number of A. odoratum plants heaved and not-heaved by frost in the first two winters at Black Birch Range, Marlborough (1370 m.a.s.l.)

Localities	FERTILIZER TREATMENTS											
	NIL				P				N + P			
	1st winter		2nd winter		1st winter		2nd winter		1st winter		2nd winter	
	Heaved	Not heaved	Heaved	Not heaved	Heaved	Not heaved	Heaved	Not heaved	Heaved	Not heaved	Heaved	Not heaved
KAIKOHE	5	1	1	0	9	3	2	2	2	9	2	8
TE AWA	9	2	0	0	7	7	2	5	2	10	1	2
LINCOLN	7	5	1	2	8	5	0	3	2	8	1	5
GORE	6	5	0	4	4	8	1	7	2	9	0	7

Based on data from inspections on 18-9-'63 (1st winter) and on 28-10-'64 (2nd winter).

of Te Awa plants of which few stayed alive. It is noticeable that especially on the NIL plots, few plants were present after the first winter. Many of them had died already before the winter set in as was observed on 14-4-'63 (see also Table 5.9.2.b). The plants used for this experiment had been broken up from plants which had previously been used for a pot experiment in a heated glasshouse and therefore it seems likely that the plants had not been hardened off sufficiently before being transferred to this site. This may explain the number of plants which died before the first winter set in. Table 5.9.2.a shows that frost-heaving severely affects plant establishment and survival: at the very best only half of the initial number of plants survived for two years. It should be kept in mind that the plants used were small plants and not locally sown plants. Worse results would have been obtained from sowings. The only self-sown seedlings which established and survived in the bare soil between plant rows, were those of Poa lindsayi.

Although the experimental area was nearly flat, solifluction was observed as a banking-up of the soil against more firmly anchored soil below this trial. In one place the banking-up amounted to 20 cm. Frost bleaching of leaves and frost-damage to panicles was also observed. Wind and rain erosion was noticed, especially on the N W side of the plants, so that it looked as if they were raised on pillars. N W winds are the prevailing winds. They are also the strongest and are frequently associated with rain. However, frost-heave appeared to be most damaging to plant establishment. Some damage to plant roots may be done by springtails which have been observed in large numbers (up to 20 per 100 cm^2) on 28-10-'64 at 8.30 a.m. As the temperature rose they disappeared rapidly so that their presence and their effect on plant

roots might have been overlooked by other observers.

The climatological table presented by Coulter (l.c.) shows that even in January the mean monthly minimum was 32°F (0°C) which suggests that frost-heaving may occur provided the soil is moist enough. It also suggests that frost damage to the panicles may occur. This causes the panicles to shrivel up. It may therefore seem surprising that sweet vernal manages to complete its life cycle at this altitude as will be shown below.

More details of survival and growth of the A. odoratum plants from four localities are shown in Table 5.9.2.b. The "number of plants" is the number of living plants which may or may not be firmly established in the soil. The "average tiller number" is the tiller number per plant and the "average culm number" is the culm number per culm bearing plant; some plants had no culms on the inspection date. No data are presented for leaf length, leaf width, and culm length since they are of limited significance.

The tiller number gives an indication of vegetative vigour of the plants. It is the highest in the N + P plots which agrees with the increase in tiller number due to N fertilizers found in experiment B (see Section 5.7.2). The addition of P fertilizers improves establishment and survival and to some degree tiller production. The tiller number of the few surviving in the NIL plot stayed constant in 1964, but in 1966 all plants were dead. The one Lincoln plant shown in the table was probably the only plant put in on 28-10-'64 which stayed alive.

It is interesting that of all the plants put in on 28-10-'64 few if any survived two summers and a winter on the NIL plots and even on the fertilized plots the results are not much better. Since the quantity of fertilizer put on at the same date was only about ¼ of the initial dressings, one has to conclude that the effect of the

TABLE 5.9.2.b Growth of A. odoratum plants at Black Birch Range, Marlborough (1,370 m.a.s.l.)

	LOCALITIES:	KAIKOHE			TE AWA			LINCOLN			GORE		
	GROWTH DATA:	A	B	C	A	B	C	A	B	C	A	B	C
NIL TREATMENT	INSPECTION DATES:												
	24- 4-1963	9	9	4	12	13	2	13	13	3	12	12	7
	18- 9-1963	4	2	.	9	5	.	7	8	.	11	8	.
	3- 6-1964	1	15	5	-	-	-	5	16	11	4	40	26
	28-10-1964	1	15	.	-	-	-	2	15	.	4	31	.
	5- 4-1966	-	-	-	-	-	-	1	3	.	-	-	-
P TREATMENT	24- 4-1963	12	9	4	12	12	3	12	8	2	11	9	2
	18- 9-1963	6	3	.	10	9	.	5	18	.	10	5	.
	3- 6-1964	6	19	10	8	20	12	3	32	22	10	19	14
	28-10-1964	3	8	.	5	25	.	3	32	.	7	24	.
	5- 4-1966	4	37	10	6	34	3	5	34	5	4	33	8
N + P TREATMENT	24- 4-1963	13	20	9	12	22	4	13	11	2	11	16	6
	18- 9-1963	9	22	.	10	31	.	9	7	.	9	20	.
	3- 6-1964	10	50	37	9	70	52	7	18	9	9	50	42
	28-10-1964	8	30	.	9	41	.	5	13	.	7	45	.
	5- 4-1966	9	25	8	4	73	30	4	26	5	7	29	13

GROWTH DATA : A = Number of living plants
B = Average tiller number per plant
C = Average culm number per culmbearing plant

The data for inspection date 5-4-1966 show the effect of replacing heaved plants on 28-10-1964.

initial dressings had worn off after two years and that the subsequent gift was insufficient for successful establishment. Adverse climatic conditions may have contributed to the poor strike of this planting.

The NIL plot results might be better than expected because of greater persistency of plants in a replicate situated between a P and a N + P plot. Some transfer of fertilizers by surface run-off from the adjoining plots may have occurred on this plot. In the remaining two NIL plots all plants had died on 3-6-'64.

The total plant numbers in Table 5.9.2.b confirm conclusions made from Table 5.9.2.a.:

(a) Gore plants survived better than the other plants on the NIL and the P plots, but on the N + P plots they are equalled by Kaikohe and Te Awa plants.

(b) P helps survival and N + P even more.

The tiller data show that:

(a) Tiller number increased during the growing season but decreased during the winter on the best fertilized plots. Apart from this seasonal fluctuation, the tiller number of most surviving plants appeared to remain fairly constant after a few years.

(b) Gore plants produce more tillers on the NIL plots than the other plants. This assists plant survival as was found by O'Connor and Lambrechtsen (l.c.).

(c) Most plants but especially those from Te Awa and Lincoln benefit from P.

(d) Kaikohe, Te Awa and Gore plants respond very well to N.

(e) Te Awa plants produce more tillers on the N + P plots

than the other plants, but half of the Te Awa plants had died by 5-4-'66.

The culm data show that flowering occurred in all populations and that "seed" formation could occur. Seedlings were found on 5-4-'66 in the plots, especially in a P plot at one end of the trial. For no apparent reason the establishment and growth of grasses and clover in this plot was much better. It was close to one corner of the fence surrounding the experimental area and might have been protected by a more lasting snow-cover or some other factor which lessened the severity of the climate. It was also possible that the subsoil was deeper and more fertile under this plot. The "seeds" and seedlings of sweet vernal found in and near this trial on that date showed that this grass completed its life cycle at this altitude although it must be close to its altitudinal limit as suggested by the paucity of seedlings even where sufficient cover was present.

However, Coulter (l.c.) has shown that the mean minimum temperature for the warmest month, January, is $0^{o}C$ and in Section 5.9.1. it has been shown that A. odoratum needs about two months of relatively frost-free weather to produce viable "seed". For these reasons, it might be assumed that the occurrence of "seeds" and seedlings of A. odoratum at this site, was due to an exceptionally mild season, and thus that under normal seasonal conditions, no "seed" would be produced by sweet vernal grass at this altitude. No climatic data were available to confirm this assumption.

The number of culms is related to the number of tillers: the more vigorous the plant, the more energy it can spend on the production of reproductive structures.

The inoculated white clover seed that was oversown at

the beginning of this experiment survived for one year in the proximity of the grass plants and then assisted in the survival of these grasses, but after two years it had survived only on the P plot mentioned before where it was well established. In fact, it tended to smother some weak sweet vernal plants. This clover cover provided a good seedbed for many cocksfoot "seeds", and some perennial ryegrass and sweet vernal "seeds". The paucity of the sweet vernal seedlings makes it likely that broadcasting sweet vernal "seed" at this altitude will not produce successful establishment unless some degree of cover is already present. The severity of high mountain climate prevents A. odoratum from displaying its colonizing characteristics. Its seedlings need some cover to become established. As pointed out by O'Connor and Lambrechtsen (l.c.), if oversown perennial ryegrass can make sufficient growth in the first year to provide some protection against frost-heave, then cocksfoot and sweet vernal plants can establish and survive while ryegrass dies back. To produce this plant succession heavy seeding rates and adequate fertilizer have to be used initially. These benefit perennial ryegrass establishment but only mulch forming grasses such as cocksfoot, sweet vernal and Yorkshire fog survive once the fertilizers have been exhausted. It appears that this mulch is indispensable for plant survival. Mulch from dead leaves produces favourable micro-climatic conditions which prevent frost-heave in the immediate vicinity of the plant and thus destruction of the roots (Gradwell, 1955, 1960); it also protects the meristematic regions.

At this altitude sweet vernal produces little mulch which disintegrates readily. Mulch has to be firmly anchored otherwise it will be blown away or disintegrate. Some plants produce firm mulch, e.g. Chionochloa species,

but especially when artificial light mulch is used, it will have to be covered with jute mesh, tar spray or something similar.

The conclusions from this experiment are:

(1) Establishment and survival of A. odoratum plants with fertilizers added but without mulching is not successful at Black Birch. Some form of mulch is indispensable. Oversown white clover cannot provide this.

(2) A. odoratum completes its life cycle at Black Birch in a favourable season but it does not spread much by "seed", nor does it form a protective soil cover. It is near or at its altitudinal limit in this locality.

(3) If A. odoratum plants establish successfully in the first year, they survive for at least three years when an initial heavy dressing of N and P is given. As the effect of these fertilizers wears off after two to three years, the plants become more subject to frost-heave and other erosion agents.

5.10 CONCLUSIONS OF HIGH ALTITUDE EXPERIMENTS

By growing A. odoratum near or above its altitudinal limit, these weaknesses in its life history were revealed:

(1) Vegetative vigour is low even after applying N and P fertilizers. It is adversely affected by grazing, short growing season, spring drought and strong, drying winds. Without fertilizers, establishment is very difficult on low fertility soils.

(2) It needs two months of relatively frost-free weather to produce flowers and to set seed. Frosts shrivel up panicles.

(3) For establishment its "seeds" need cover to provide moisture and to prevent frost-heave.

(4) It does not produce sufficient mulch in which other plants can become established. Its mulch disintegrates readily under the influence of wind, frost, snow, rain and limited microbiological activity.

Any one or a combination of the above points will limit the ascent of A. odoratum in mountains. However, at lower altitudes where these weaknesses are not revealed, A. odoratum is a colonizer and a persistent plant as shown in Chapters 2 and 4.

5.11 SUMMARY OF CHAPTER 5

The experiments designed to determine the reactions of A. odoratum to various environmental influences the yielded following results:

(1) Physiological races exist among A. odoratum plants from different parts of New Zealand. The Kaikohe plants contain winter-active plants, whereas the Porter's Pass plants contain winter-dormant plants.

(2) A. odoratum behaves like other festucoid grasses with respect to rootgrowth, tiller production and rate of leaf appearance although its herbage production is low.

(3) When grown in association with Agrostis tenuis and Holcus lanatus, the tiller production of A. odoratum is not affected, but its herbage production is reduced, especially when grown with H. lanatus.

(4) The effect of fertilizers on tiller and herbage production of A. odoratum is:

(a) N : first a depression then a marked response

(b) P : very low response

(c) S : depression of tiller number but no effect on herbage production.

(5) The effect of cutting on herbage production of A. odoratum is:

(a) When cut from 10 to 3 cm total leaf harvest higher than total stubble harvest.

(b) When cut from 15 to 6 cm, total leaf harvest lower than total stubble harvest.

(c) Total leaf + stubble yield higher in (b) treatment than (a).

(6) The altitudinal limit of A. odoratum is determined by several environmental factors which affect its life history as follows:

(a) vegetative vigour is much reduced by low soil fertility and short growing season,

(b) flower production and seed setting is prevented by frost,

(c) seedling establishment is prevented by frost-heave and lack of cover.

CHAPTER 6

INDICATOR PLANT EXPERIMENT

6.1 INTRODUCTION

For a long time, leaf analyses have been used as indicators of the response to or need for fertilizers (Lundegardh, 1951) and from this, the idea was developed of using plants as indicators of element availability on different soils. In New Zealand, A. odoratum has been used for that purpose (Wells, 1956a, b, 1957; Wells and Saunders, 1960), because it occurs on a very wide variety of soils, is readily distinguished when flowering and its depth of rooting is similar to that of most plants of agricultural importance. It was noted that plants would have to be sampled at a certain stage of growth, because of considerable seasonal variability in chemical composition. It seemed that provided a standard sampling procedure was adopted, and contamination especially with soil was avoided, this technique could successfully be used to assess the nutrient availability in soils throughout New Zealand. Since plant species differ widely in their nutrient uptake, it may be argued that the use of only one indicator species must necessarily give indications of rather limited value. But as long as this is kept in mind, one indicator species is better than none.

However, for many years it has been known that not only species but also varieties within a species may vary considerably with regard to element uptake as is shown by the review articles of Millikan (1961), Vose (1963) and Whitehead (1966). Recent investigations to explain the processes of adaptability and adaptation have been made by Grant (1963) and Wardlaw (1965) (see Section 10.3). Reciprocal transplant studies carried

out by Bradshaw, Snaydon and co-workers have demonstrated that populations of Trifolium repens and Festuca ovina become adapted to their environments, especially soils, which is expressed by differential uptake of Ca, P and K (Bradshaw and Snaydon, 1959; Bradshaw et al.,1960; Snaydon, 1962, a, b, c; Snaydon andBradshaw, 1961, 1962 a, b). They showed that T. repens populations from acid soils grew better in upland Festuca/Agrostis swards than similar populations from calcareous and from medium-fertility soils. F. ovina populations from acid, low Ca soils showed a weak response to Ca, while those from calcareous soils showed a strong response.

Gregory and Bradshaw (1965) have shown that populations of Agrostis tenuis and one of Anthoxanthum odoratum can be found growing in conditions of metal contamination toxic to most higher plants. An index of tolerance was obtained (using the method of Jowett 1958, 1964) by measuring the rooting of tillers of tolerant and of control populations in solutions with copper, nickel, lead and zinc, and in control solutions. An A. odoratum population from a zinc-lead mine had an index of tolerance for zinc of 75.1%, while the control plants had an index of 2.3%. Gregory and Bradshaw suggest that the tolerance mechanism may ultimately be found to be analogous to that for aluminium and they state that "Jones (1961) has found that the tolerance of some species to aluminium can be correlated with their capacity to immobilize the metal and suggests an organic acid buffer system". In three examples, Jain and Bradshaw (1966) showed that very sharp transitions occurred in populations of A. tenuis and A. odoratum near mines in Wales: over a few metres a change from fully tolerant to non-tolerant plants could be demonstrated. In a further example from the Park Grass plots at Rothamsted, they showed that a

marked change in size of A. odoratum plants collected from limed and unlimed sub plots occurred. Snaydon (1963) had already demonstrated that significant morphological and physiological differences existed among samples of A. odoratum from the various Park Grass plots.

For these reasons, it was thought to be very likely that similar differentiation might have occurred among the groups of A. odoratum plants discussed in previous chapters.

Nutrient uptake is a metabolic process and hence environmental factors such as light and temperature have been found to affect the chemical composition of plants; for examples, see Bathurst and Mitchell (1958) who studied nine pasture plants in New Zealand and the review article by Whitehead (l.c.).

Unpublished results from a pilot experiment with two clones of A. odoratum: One from a Porter's Pass plant and one from a Gore plant; with several levels of N, P and S fertilizers and grown in pots filled with a high country soil from Enys Flat, Broken River area, Canterbury, had shown decisive differences between the clones in their response to these fertilizers. The results were based on leaf weight and tiller number data. They suggested that positive results might be obtained from the experiment described below.

6.2 MATERIAL AND METHODS

A. odoratum plants which had been used for the Experiment II, described in Section 2.6.3, were broken up into clumps of about four tillers and planted in boxes filled with horticultural sand on 16 to 18 April 1964. Four plants each of the following localities were used: Kaikohe (K), Te Awa (TA), Lincoln (L), Gore (G) and Porter's Pass (PP); each plant was broken up into

clumps to provide sixty identical plants (thirty per site), which were watered with tapwater only. In this way, no fertility or adaptation effect from previous treatment was likely to be carried over and most differences shown in this experiment could be attributed to genetically fixed characteristics in the plants.

The plants were grown at two sites:

A : Ilam, on the experimental grounds of the Botany Department, University of Canterbury, Christchurch. The soil is a low fertility Waimakariri fine sandy loam.

B : Lincoln, on the experimental grounds of Grasslands Division, D.S.I.R., Substation Lincoln. The soil is a high fertility Templeton silt loam.

From soil samples taken on 6 October 1965 at Ilam and on 21 October 1965 at Lincoln, the following analyses have been supplied by Mr N. Wells, Soil Bureau, D.S.I.R., Lower Hutt.

TABLE 6.2.a Soil tests of experimental grounds

	PH H_2O	P $N.H_2SO_4$	C.E.C. me %	T.E.B.	Ex.Ca	Ex.Mg	Ex.K	Ex.Na
ILAM	5.77	15.4	14.8	9.5	7.2	1.8	0.4	0.2
LINCOLN	6.26	42.6	13.1	9.3	7.6	1.0	0.5	0.2

No fertilizer has been applied before or during the experiment.

On 11 September 1964, six hundred plants were planted out in a randomized pattern in six rows of five identical plants at Ilam as single plants in a 60 cm x 60 cm planting grid, and on 4 November 1964, a similar number was planted

out in a similar manner at Lincoln.

Harvesting took place when the panicles had emerged but the stamens were not yet visible. This stage corresponds approximately to stage 5 as defined by Wells (1956a). The plants at Lincoln were sampled from 21 September to 9 November 1965 and those at Ilam from 6 October to 17 November 1965. The plants flowered in approximately the same sequence at both sites. A large handful of herbage was cut with shearing shears from the middle of a plant, 3 cm above soil level. The samples from identical plants were mixed, botanically analysed, dried at 80°C in a forced draught oven, ground in a Cassella herbage grinder and stored in waxed oyster pottles.

6.3 RESULTS AND DISCUSSION

Analyses were carried out by Mr N. Wells, Soil Bureau, D.S.I.R., for the following elements: K, P and S. This range is rather limited when compared to the large number of elements for which Mr Wells (pers. comm.) has used A. odoratum during his study of element availability in 250 New Zealand soils; the results are presented in Table 6.3.a.

From these data, decisive differences were found for P between the soil types and the localities, and for S among the localities. This shows, that in spite of the elaborate precautions taken, genetically fixed adaptations occur among A. odoratum plants, in particular between the montane Porter's Pass plants and the remaining plants from the lowland localities for the elements P and S.

To explain this phenomenon, the following assumptions may be made:

TABLE 6.3.a Chemical analyses of Anthoxanthum odoratum plants grown at two sites: Ilam and Lincoln.

The data for each plant are based on 30 clones per plant per site.

	Plant	%K		%P		%S	
		Ilam	Lincoln	Ilam	Lincoln	Ilam	Lincoln
Kaikohe	1	2.20	2.26	.13	.30	.16	.16
	2	2.27	2.17	.19	.30	.17	.18
	3	2.27	2.28	.17	.34	.18	.18
	4	2.72	2.73	.19	.32	.17	.18
	Av.	2.37	2.36	.17	.32	.17	.18
Te Awa	1	1.98	2.20	.17	.30	.16	.15
	2	2.26	2.33	.16	.29	.14	.14
	3	2.08	2.08	.20	.31	.19	.18
	4	2.52	2.82	.14	.30	.18	.17
	Av.	2.19	2.36	.17	.30	.17	.16
Lincoln	1	2.45	2.33	.15	.32	.17	.16
	2	2.15	2.45	.13	.31	.16	.15
	3	2.34	2.54	.16	.34	.15	.14
	4	2.55	2.75	.16	.30	.18	.16
	Av.	2.37	2.52	.15	.32	.17	.15
Gore	1	2.33	2.37	.18	.29	.17	.18
	2	2.02	2.61	.16	.28	.16	.16
	3	2.57	2.60	.18	.32	.18	.19
	4	2.16	1.88	.16	.31	.16	.17
	Av.	2.27	2.37	.17	.30	.17	.18
Porter's Pass	1	2.41	2.40	.20	.35	.19	.18
	2	2.55	2.32	.19	.37	.19	.20
	3	2.32	2.48	.23	.36	.20	.19
	4	1.90	2.33	.17	.34	.15	.23
	Av.	2.30	2.38	.20	.36	.18	.20

ANALYSIS OF VARIANCE:

Between:	K	P	S
Soils	n.s.	xx	n.s.
Localities	n.s.	xx	xx
S.e. of loc. mean		.0064	.00555
L.S.D. 5%		.020	.016
L.S.D. 1%		.026	.022

(1) the Porter's Pass plants have been established from seed which was very different in origin compared to that which gave rise to the lowland plants,

(2) the Porter's Pass plants, being winterdormant (see Section 5.4), have a more efficient uptake mechanism at low temperatures than the more or less winteractive lowland plants,

(3) the Porter's Pass plants have adapted themselves to the low fertility Kaikoura steepland yellow-brown earth on which it grows; this soil is low in P and S.

Although the Porter's Pass plants have been found to possess winterdormant features, their rate of development at the two experimental grounds was similar to that of the other populations, so that no temperature effect due to later development could have caused the higher values for P and S found in these montane plants.

In view of the work of Bradshaw and Snaydon, discussed in Section 6.1, it is most likely that the higher uptake of P and S in the Porter's Pass plants was the result of adaptation to low fertility as suggested in (3). The absence of significant differences in K uptake among the plants could be explained similarly: because none of the plants originated from low K soils, there was no stress or selective pressure for this element and therefore no differences in K uptake could be expected. Overall there was a slight tendency for the average K values to be higher at Lincoln than at Ilam, which might be reflected by the K values in Table 6.2.a.

Gregory and Bradshaw (1965) found very considerable variability between clones within a population: in their Table 5, six clones of Agrostis tenuis from a mine in Wales had tolerance indices varying from 28.3 to 82.7 for zinc, and another six clones of A. tenuis from a pasture

had indices of 2.0 to 19.6 for copper.

The variability among the four plants from the five localities, evident in Table 6.3.a, is not as considerable as that found by Gregory and Bradshaw, but it is often significant at 5% level.

The following significant correlations between all K, P and S values were found:

ILAM	% K	x	LINCOLN	% K	:	r =	.56**
ILAM	% P	x	LINCOLN	% P	:	r =	.50*
ILAM	% S	x	LINCOLN	% S	:	r =	.42*
ILAM	% P	x	ILAM	% S	:	r =	.49*
LINCOLN	% P	x	LINCOLN	% S	:	r =	.51*
ILAM	% K	x	ILAM	% S	:	r =	.44*

All other combinations showed insignificant correlations.

The correlations between the two sites for the same element show that the plants have not changed their adsorption mechanisms for these elements while growing at the two sites. The significant correlations between the uptake for P and for S at each site suggest that there is a similarity in the uptake mechanism for P and for S. The lack of correlation between the uptake of K and that of P and S, except for the correlation Ilam K x Ilam S, suggests that the cation K is taken up by a different process. No explanation can be offered for the correlation Ilam K x Ilam S.

A recent review of the processes involved in ion uptake by plants from soil (Anon., 1966) shows that although very many facts have been produced on ion uptake, no clear general picture has yet emerged. This may be due to:

(1) different plants used,

(2) different ages of the plants used,

(3) different parts of the plants used : whole plants, excised roots or root discs,

(4) different media used : nutrient solution or soil,

(5) different processes occurring in different tissues,

(6) the effect of micro-organisms on nutrient uptake (Barber and Loughman, 1967).

For these reasons, it is felt that a detailed discussion of ion uptake mechanisms is not justified here.

Gregory and Bradshaw (l.c.) observed that most populations of A. tenuis and some other grasses, tolerant to normally toxic levels of heavy metals (Cu, Zn, Ni, Pb), occurred in mining regions where it was likely that toxic conditions had existed for a long time due to seepage etc., from rocks. The toxicity of the lower Swansea site was, however, entirely due to smelting of imported ore; no pre-existing ore deposits occurred in this region. They concluded: "It is, therefore, likely that this population represents the evolution of a tolerant population in historic times". In a similar manner, the montane plants from Porter's Pass, appear to have become adapted to their environment in less than one hundred years.

The chemical analyses of the herbage for P from the two sites have a ratio of about 1 : 2, while the soil tests for P have a ratio of about 1 : 3, which illustrates that the determination of P with N H_2SO_4 bears little correlation with P, readily available to plants.

6.4 CONCLUSION AND RECOMMENDATION

Although only three elements have been determined and although plants from only one locality out of five behaved differently in this experiment, it is considered that the evidence from the literature reviewed and from the experiment discussed in this chapter, is sufficient

to reach the following conclusions and recommendations:

(1) A. odoratum plants have genetically fixed differences in element uptake from soils.

(2) A. odoratum plants from a montane locality take up decisively different amounts of P and S when compared to plants from four lowland localities.

(3) The determination of the quantity of an element present in the soil by means of a soil test and by means of a chemical analysis of A. odoratum plants shows some correlation.

(4) Serious doubts may be raised about the usefulness of the highly variable and adaptable outbreeder A. odoratum as an indicator plant of element-availability in different soils if local plants are used. These doubts could be eliminated by using several clones of A. odoratum plants from widely differing soil types, and by planting them in the soil types to be tested along the lines described in this experiment.

(5) Since plants differ widely in their nutrient uptake, it is suggested that two physiologically different plant species should be used as indicators of element availability in soils e.g. Trifolium repens and A. odoratum. The difference in chemical composition of T. repens and Agrostis tenuis for the elements Ca, K and P illustrates this point (Snaydon, 1962a, Table 6).

CHAPTER 7

MORPHOLOGICAL DIFFERENCES

7.1 INTRODUCTION

The evidence from the experiments described in Chapters 2, 5 and 6, showed that physiologically distinct plants of the outbreeder A. odoratum exist in New Zealand. In this Chapter, the presence of morphological differences among sweet vernal plants from different localities is investigated.

Baker (1959) points out that in any environment outbreeders may show great variation from plant to plant and that even under selective pressure, this relatively continuous variability within a population of an outbreeder will tend to obscure any clear-cut distinctions between populations. However, Bradshaw's (1959) studies of the outbreeder Agrostis tenuis showed that distinctions between populations could be recognized. This species has a more or less continuous distribution in Central Wales, but clines of varying slopes interspersed with rather sharp discontinuities corresponding to changes in the environment occur; this pattern of variation, Bradshaw calls a "graded patchwork". In my opinion this is a good term because it emphasizes not only the erratic distribution of distinctive populations, but also the difference in intensity of distinctive features in these outbreeding populations. From field observations, it appears that A. odoratum also forms such a graded patchwork but no extensive field collections have been made to confirm this.

A. odoratum plants, collected from five different parts of New Zealand, have been investigated for certain morphological features.

These investigations were carried out on plants established in a common environment. The plants were

either direct transplants from the collection sites or seedlings raised from seed collected at these sites. On the same plants flowering studies have been carried out (see Section 2.7.1). The observations were made for two successive seasons on the direct transplants and for only one season on the plants raised from seed.

7.2 MATERIAL AND METHODS

Plants from five localities in New Zealand - Kaikohe, Te Awa, Lincoln, Gore and Porter's Pass (for description of sites, see Appendix A) were obtained in the autumn of 1962 and were planted at Ilam in the experimental grounds of the Botany Department, University of Canterbury on 22 May 1962. The plants were put in rows of 22 single plants in a 60 x 60 cm planting grid. These direct transplants will be referred to as "Block A".

The following numbers of plants were used:

Kaikohe (K) : 44 plants
Te Awa (TA) : 11 plants
Lincoln (L) : 33 plants
Gore (G) : 11 plants
Porter's Pass (PP) : 22 plants

The plants raised from seed, gathered at the five collection sites, and sown in May 1962, were planted in the same area at Ilam on 25 August 1962. Enough seed for this part of the experiment was available from only four localities: Kaikohe, Te Awa, Lincoln, Gore. Twenty two plants from each locality were planted out in the manner described before. These plants raised from seed will be referred to as "Block B".

All the plants were kept reasonably free from weeds by inter-row cultivation with a rotary-hoe, were trimmed back with shears in autumn and then topdressed with a

mixture of DDT-superphosphate and sulphate of ammonia. Occasionally the plants required sprinkling with water to keep them alive in the middle of summer.

On each plant, all culms were counted ("culm number"), the length from base of plant to tip of panicle was determined on 50 culms ("culm length"); and the length from the lowermost node of the panicle to the tip was determined on 50 panicles ("panicle length"). The first two measurements were taken in the field; the last one in the laboratory. This field work was done when the panicles had yellowed, culm elongation had stopped and most "seed" had been shed; it usually took from the middle of December to the middle of January. Statistical tests for standard deviation showed that a sample of 50 was representative (for culm length σ ranged from 3.81 to 7.30 and for panicle length from 4.85 to 13.89).

7.3 RESULTS AND DISCUSSION

To determine morphological differentiation in the plants from these five localities, analyses of variance were carried out on the plants arranged in multiples of 11. For this, each row was simply divided into two, and although this did not make each half a replicate, the analyses were greatly simplified and at the same time some indication of within-locality variability was obtained.

For the sake of clarity only the final summaries are shown in Tables 7.3.a, b, c for the plants in "Block A" and in Tables 7.3.e, f, g for the plants in "Block B". The seasons 1963 and 1964 refer to the summers of December 1962 - January 1963 and December 1963 - January 1964 respectively.

TABLE 7.3.a Culm numbers of Anthoxanthum odoratum plants in Block A

SUMMARY OF ANALYSIS OF VARIANCE

Source of variation	1963	1964
Within K	*	N.S.
Within L	N.S.	N.S.
Within PP	N.S.	N.S.
Within localities	**	**
Within blocks	N.S.	N.S.

OVERALL MEAN PER PLANT

Localities	1963	1964
Kaikohe	420	448
Te Awa	402	283
Lincoln	74	267
Gore	345	173
Porter's Pass	285	383
s.e.	38.3	56.8

TABLE 7.3.b Culm lengths in cm of Anthoxanthum odoratum plants in Block A

SUMMARY OF ANALYSIS OF VARIANCE

Source of variation	1963	1964
Within K	*	N.S.
Within L	*	N.S.
Within PP	N.S.	N.S.
Within localities	**	**
Within blocks	N.S.	**

OVERALL MEAN PER PLANT

Localities	1963	1964
Kaikohe	54.6	53.2
Te Awa	55.2	57.8
Lincoln	65.2	65.5
Gore	50.9	58.0
Porter's Pass	55.7	53.3
s.e.	1.63	1.53

TABLE 7.3.c Panicle lengths in mm of Anthoxanthum odoratum plants in Block A

SUMMARY OF ANALYSIS OF VARIANCE

Source of variation	1963	1964
Within K	N.S.	N.S.
Within L	N.S.	*
Within PP	N.S.	N.S.
Within localities	**	**
Within blocks	N.S.	N.S.

OVERALL MEAN PER PLANT

Localities	1963	1964
Kaikohe	62.3	49.7
Te Awa	64.4	56.1
Lincoln	81.9	56.0
Gore	67.7	58.1
Porter's Pass	66.1	51.5
s.e.	2.93	1.54

Since the direct transplants have been observed for two years the measurements in Tables 7.3.a, b, c provide some indication of the plasticity of the plants. The changes in culm number (Table 7.3.a) are especially striking in the Lincoln and Gore plants. It may be that the Lincoln plants which originated from a dense, undisturbed stand of tall grasses could increase their tiller number and therefore their culm number successfully as single plants in the absence of competition; the Gore plants may have suffered from drought which resulted in the decrease in culm number in the second season. However, the age of the individual plants may have had a more pronounced effect on the variability of culm number than certain environmental factors.

The culm length (Table 7.3.b) remained fairly constant for plants from most localities although that of the Gore plants had increased significantly by 1964. The variation within the blocks of eleven plants was decisive, however, so that the significance of the overall mean culm length figures for the 1964 season may be limited. Nonetheless, in that season the culms of the Lincoln plants were still 7.5 cm longer at an average than those of the next longest which may be due to its original habitat: a dense stand of tall grasses.

The panicle length (Table 7.3.c) levelled out in the second season; in the first season the Lincoln plants had very much longer panicles which may again be a reflection of their original habitat: in a stand of tall plants, it is more advantageous to have large panicles if only few culms can be formed, than to have small ones if a satisfactory amount of seed is to be produced for survival and spread. The rapid levelling out of panicle length in the plants from these five localities suggests that this feature is not very constant.

The correlations between the data presented in the previous three tables have been summarized in Table 7.3.d. The absence of any regularity in the pattern of correlations

for different measurements within a locality emphasizes that these plants still possessed a more or less continuous variability characteristic of outbreeders - the Porter's Pass plants being the least stable and the Kaikohe plants the most stable. However, the latter may only appear to be more stable because of the higher number of plants observed, which gave rise to more statistically significant correlations. It is interesting to note that the Porter's Pass plants are the least stable morphologically which may suggest that these plants have not been in this environment very long or that the changeability of mountain climate promotes adaptability. On the other hand, physiological differences among these plants have been demonstrated in Chapters 2, 5 and 6 which may suggest that physiological adaptations occur more rapidly than morphological ones. This possibility will be considered in more detail during the discussion on the presence of ecotypic differentiation in A. odoratum in New Zealand (see Chapter 10).

The culm number counts carried out in the 1964 season on the plants sown from seed in "Block B" (Tables 7.3.e, f, g) show a trend which approximates that of the plants in "Block A" in the 1963 season - only the Lincoln plants are noticeably different. Unfortunately, no measurements have been carried out in the 1965 season to see whether these differences would level out as occurred in the 1964 season in the "Block A" plants. On the other hand, there may have been an increased effect of plant age and viruses which would have made comparison with the plants in "Block A" more difficult. The other features measured - culm length and panicle length had already evened out by 1964 so that a statistically significant difference was absent. This was largely caused by viruses. Their effect was especially noticeable in three Lincoln plants as it depressed culm length and may have reduced panicle length. If these three plants had had measurements comparable to the remaining plants, a

TABLE 7.3.d Summary of correlations between measurements presented in Tables 7.3.a, b, c

	Localities				
	K	TA	L	G	PP
Culm numbers 1963 x 1964	N.S.	N.S.	**	*	N.S.
Culm lengths 1963 x 1964	**	N.S.	N.S.	N.S.	N.S.
Panicle lenghts 1963 x 1964	**	N.S.	*	N.S.	N.S.
Culm length x panicle length 1963	**	*	N.S.	N.S.	N.S.
Culm length x panicle length 1964	**	N.S.	N.S.	N.S.	N.S.
Culm length x culm number 1963	N.S.	N.S.	**	N.S.	N.S.
Culm length x culm number 1964	N.S.	N.S.	→*	**	N.S.

TABLE 7.3.e Culm numbers of Anthoxanthum odoratum plants in Block B

SUMMARY OF ANALYSIS OF VARIANCE		OVERALL MEAN PER PLANT
Source of variation	1964	
Within Kaikohe	N.S.	458
Within Te Awa	N.S.	314
Within Lincoln	N.S.	197
Within Gore	N.S.	443
Within localities	**	s.e:
Within blocks	N.S.	37.8

TABLE 7.3.f Culm lengths in cm of Anthoxanthum odoratum plants in Block B

SUMMARY OF ANALYSIS OF VARIANCE		OVERALL MEAN PER PLANT
Source of variation	1964	
Within Kaikohe	N.S.	54.5
Within Te Awa	N.S.	50.9
Within Lincoln	N.S.	56.6
Within Gore	N.S.	54.6
Within localities	N.S.	
Within blocks	N.S.	

TABLE 7.3.g Panicle lengths in mm of Anthoxanthum odoratum plants in Block B

SUMMARY OF ANALYSIS OF VARIANCE		OVERALL MEAN PER PLANT
Source of variation	1964	
Within Kaikohe	N.S.	54.2
Within Te Awa	N.S.	54.4
Within Lincoln	N.S.	58.9
Within Gore	N.S.	55.2
Within localities	N.S.	
Within blocks	*	

TABLE 7.3.h Summary of correlations between measurements presented in Tables 7.3.e, f, g

	LOCALITIES			
	K	TA	L	G
PANICLE LENGTH X CULM LENGTH	N.S.	N.S.	**	N.S.
CULM NUMBER X CULM LENGTH	N.S.	N.S.	*	*

statistically significant difference between the Lincoln plants and those from the other three localities would have been obtained for culm length and possibly for panicle length as well. This suggests that there is a trend for the morphological differences observed in the Lincoln group of plants to become genetically fixed. Table 7.3.h shows that some correlation exists between the three features measured in the Lincoln plants, which may support the observed morphological distinctness of this group of plants.

Strelkova (1932) studied A. odoratum in 10 plant communities in the Leningrad district. One of these, her Scirpeto crepetum, a community of tall mixed grasses with large leaves, appeared to be rather similar to the Lincoln sample site, since the sweet vernal plants in that community had mostly long panicles, were tall with broad, long leaves and few tillers, just like the Lincoln plants. Her plant communities from rather dry meadows contained A. odoratum plants which compared favourably with those from my remaining lowland localities - Kaikohe, Te Awa and Gore: panicles mostly of medium size, medium-sized plants with short leaves and more tillers. Strelkova stresses that A. odoratum reacts very quickly to different environmental conditions. Plants from different habitats, transferred to uniform nursery conditions, had already lost many of their earlier distinguishing features after one year and they started to look alike. Some had lost their original form altogether, while others retained their distinctive features but turned into more luxuriant nursery type plants. Strelkova was of the opinion that the stability of various taxonomic features could only be determined from rather lengthy experiments and she found that two seasons of observations in a nursery were too short to make a full analysis and evaluation of distinct forms. In earlier work on A. odoratum, Rozanova (1926) showed that the environmental factors which affect the variability of a morphological character are different for each character and that the

effect sets in earlier for some characters than for other ones. From their work on Agrostis stolonifera, Ashton and Bradshaw (1966) reached similar conclusions.

The variability and plasticity of the outbreeder A. odoratum make it difficult to reach definite conclusions on the existence of morphologically distinct groups of plants in New Zealand; insufficiently large samples from each locality increase these difficulties. Davies and Heywood (1963, p.407) quote Clausen who recommends seed sampling as the best method to give an adequate impression of variability in a group of plants rather than direct transplants. When seed sampling is used, seed should be obtained from 60 - 100 plants per locality, 300-600 seedlings should be raised from which about 120 should be pricked out. For his study on morphological differentiation in populations of Agrostis tenuis, Bradshaw (1959) collected 60 tillers per site of about 30 by 30 metres. He preferred tillers because firstly, they are samples of what is actually present, established in the sward, after the intervention of natural selection; secondly, seed is difficult to obtain in a region that is heavily grazed and biased sampling may occur if only one or two panicles which have escaped grazing are picked, since these are likely to belong to prostrate plants. It is clear that there are merits in both kinds of sampling: tillers of direct transplants give an impression of the variability in the genotypes surviving under local conditions, whereas seed (especially from outbreeding plants) gives an impression not only of the variability among the genotypes surviving under local conditions of competition and natural selection, but also of the variability in new genotypes which may survive if these local conditions change. Therefore seed sampling gives a more complete picture of the differentiation potential in a group of plants. This is very important when studying A. odoratum which relies heavily on seed-production to maintain itself in a plant community and to colonize new areas.

Although samples of A. odoratum plants from each locality could have been larger which would have increased the significance of the results presented in Tables 7.3.a - h, the differences between the figures obtained for the direct transplants ("Block A") and the seedlings ("Block B") are considerable. Ashton and Bradshaw (l.c.) also observed marked discrepancies between similar plants from Agrostis stolonifera populations. They considered that these "discrepancies between seed and adult samples not only offer evidence for gene flow but also per contra for selection. If selection were not acting, the adult populations would resemble the seedling populations. Therefore, there must be directional selection counteracting the effects of gene flow ...". They also suggested that "there must be stabilizing selection, maintaining the low level of variability of the adults: this is probably due to the superiority of a few clones in the populations, causing them alone to occupy the habitat". Whether a similar stabilizing selection is present among the direct transplants of A. odoratum for the characters observed, cannot be determined. Since sweet vernal has only a restricted perenniality (see Section 2.11), it is likely that stabilizing forces make less impact on A. odoratum populations than on those of Agrostis stolonifera which has strong powers of vegetative propagation by means of its stolons. However, directional selection in spite of considerable gene flow has led to the observed morphological differences in the Lincoln plants of A. odoratum.

The ability of the outbreeder A. odoratum to differentiate into more or less distinct local groups of plants regardless of strong gene flow confirms its fitness as a colonizer; individual groups of plants are regularly invigorated by the formation of new genotypes which enable this plant not only to maintain itself in a plant community but also to invade new habitats. Ashton and Bradshaw (l.c.) formed similar conclusions from their

work on Agrostis stolonifera and stated that "such evolutionary change is not only adaptive, it is also permissive".

7.4 CONCLUSIONS AND SUMMARY

(1) Although A. odoratum has been in New Zealand now for about one hundred years, it is still a highly variable plant from a morphological point of view.

(2) Transplants are rapidly modified by experimental garden conditions, especially with regards to culm number and panicle length.

(3) Plants from seed may be even more rapidly modified by experimental garden conditions.

(4) The morphological differences observed in the Lincoln group of plants tend to become genetically fixed.

(5) The montane Porter's Pass plants are more adaptable than all other plants studied.

(6) Larger numbers of plants from seed should have been used per locality.

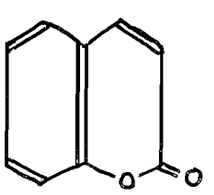
(7) The plants should have been observed for a longer period although the increasing effect of plant age and viruses would have made annual comparisons more difficult.

CHAPTER 8

COUMARIN

8.1 INTRODUCTION

Anthoxanthum odoratum is well known for its smell of "newly mown hay" which gives it its specific name odoratum. The smell is due to the presence of coumarins, some of which have been identified by Davies and Ashton (1964). Heeger and Poetke (1954) state that the smell of "newly mown hay" is released by a hay bacterium: Bacterium subtilis which produces fermentation which occurs in all grasses during drying. The presence of coumarin made sweet vernal very sought after as the supplier of "essence de flouve odorante", which was used in the perfume industry (Weber, 1960) until a method of synthesis was evolved. Coumarin is an unsaturated lactone with the following structure:



8.2 COUMARIN IN ANTHOXANTHUM SPECIES

Experiments carried out by Davies et al. (1962) on A. odoratum in vegetative state showed that at maturity the leaves had a peak value for coumarin and also for related compounds. With senescence the coumarin value in each leaf decreased, but that of the related compounds after an initial fall, increased to a second maximum. In the species A. puelii* and A. amarum, which flowered

*Maire (1953), according to Borrill (1963) considers that A. puelii Lec. et Lam. and A. aristatum Boissier are synonyms, and since the latter was described earlier it has priority. But Stearn and Gilmour (1932) say that A. aristatum is more closely related to A. ovatum Lag.

under the same experimental conditions, the content of coumarin and related compounds increased in successive mature leaves on the main stem. The flag leaf had a maximum value. Greater concentrations of coumarin and related compounds were found in the leaves of A. amarum than in those of A. puelii, up to 4% and 0.8% coumarin respectively. In A. odoratum the highest value found was 3.4%.

Ashton and Jones (1959) report that the seeds of sweet vernal contain no coumarin and that it makes its first appearance in the seedling when the green plumule emerges. No coumarin was found in sweet vernal seedlings grown in the dark.

8.3 PHYSIOLOGICAL EFFECTS OF COUMARIN

Bose (1958) has reviewed some physiological properties of natural coumarins but in this section only a few effects of coumarin on animals and plants will be discussed.

8.3.1 Effects on animals and man

Coumarins are found in many other plants (Hegnauer, 1962-64) and where they occur in pasture plants, they may give rise to animal diseases. A large amount of research has been and is still being done on the "sweet clover disease" which occurs fairly frequently in Canada and the U.S.A. when animals eat spoilt hay of sweet clover (Melilotus alba and other species). When this hay becomes mouldy, coumarin and/or its derivatives are converted into dicoumarol, whose anticoagulant properties cause sweet clover disease in cattle and sheep. It is characterized by haemorrhages which are often fatal. In view of this, Davies and Ashton (l.c.) investigated the possibility of spoilt sweet vernal hay causing similar metabolic disorders. Although the coumarins and related

compounds were virtually the same in sweet vernal and in sweet clover, they found that the concentration of these compounds was more than twice as high in sweet clover as in sweet vernal hay after spoilage. From this and from the results of earlier experiments in which spoilt sweet vernal hay, and grasses sprayed with up to 1% coumarin on a dry matter basis, were fed to sheep and rabbits, Davies and Ashton (l.c.) concluded that it is unlikely that the increased use of Anthoxanthum species in pastures would lead to detrimental effects. However in his review article, Soine (1964) lists various activities attributable to coumarins: oestrogenic, dermal photo-sensitizing, vasodilator, sedative and hypnotic, hypo-thermal, antibacterial, antifungal, molluscacidal and several others. Therefore, it is possible that sweet vernal grass or hay does affect animal metabolism in a way at present not yet diagnosed. In New Zealand less facial eczema spores were counted on sweet vernal leaves than on those of other grass species (Anon, 1960), which is just another example of the antifungal activity of coumarins.

8.3.2 Effects on plants

Coumarins are well known as seed germination inhibitors and are often used in laboratory experiments. They will inhibit the germination of lettuce seeds in the dark (Evenari et al., 1954) but French workers found that they speed up the germination of seeds of A. odoratum and Melilotus officinalis (which also contains coumarin) very markedly (Hocquette et al., 1956). The stimulation of germination is more marked as the concentration of the coumarins increases, but Hocquette et al. (l.c.) do not present data to support this statement.

Coumarins also affect root growth. Goodwin and

Taves (1950) showed that rootgrowth of Avena seedlings nearly stops at a coumarin concentration of 10^{-3} M. In the period 6 - 18 hours after treatment with 10^{-3}M coumarin, the growth rate of the Avena roots fell to 5% of that of the controls.

A research team in Germany has tried to establish whether coumarins secreted by one plant could adversely affect the growth of others. Knapp and Furthmann (1954) found little evidence for this when they grew seedlings of Melilotus alba and Lolium murinum together in petrie dishes or as plants together in pots. From the work of Grimm (1953), it could be suggested that this was due to bacterial activity which results in breakdown of coumarins. That this occurs very rapidly in the soil is evident from the statement of Hawker et al. (1960, p.275): "The seed germination inhibitor, coumarin, is also swiftly decomposed by soil micro-organisms". Rivière and Chaussat (1966) found such micro-organisms in soils under permanent pasture containing A. odoratum, but not in arable soils. 16.2% of the strains of micro-organisms found in the rhizosphere of A. odoratum were able to destroy coumarin, whereas only 4.3% of those in the wheat rhizosphere could do so. In more involved experiments, mostly based on the circulating water culture technique developed by Börner (1958), some evidence was obtained for allelopathy, the effect of one higher plant upon another (Börner, 1960; Rademacher et al., 1961). Although 57 plant combinations were investigated, no experiments were carried out with A. odoratum.

Coumarin is excreted by the roots of sweet vernal (Troughton, 1957, p.51), which was also found by me during sampling of dry soil in a stand of sweet vernal, and whenever the roots of such plants were broken up. Some plants appeared to have higher coumarin concentrations

than others which has already been shown by Ashton and Jones (1959, Table 2). Coumarin in dry soils may have some effect on other plants, but this would be hard to separate from ordinary drought stresses.

Knösel (1959) examined the effect of p-coumaric acid and two other phenolic substances on fungi, streptomycetes and bacteria in the soil. Fungi in particular were able to break down these compounds but streptomycetes and bacteria could not do this to the same extent in nutrient solutions. When the phenolic substances were added to soil probes, the results were rather varied. Soil fungi and bacteria were not distinctly influenced but streptomycetes increased in numbers. From these experiments it appears that there is a slight effect of these coumarins on soil micro-organisms. Because of this effect and that observed on root growth and the germination of seeds, coumarins may play a role in the competitive ability of sweet vernal grass and may thus help to explain its position in plant communities. Therefore it is worth looking in more detail into the coumarins present in A. odoratum and their effect on plants and animals.

8.4 SUMMARY

(1) Coumarin which is present in both roots and shoots of A. odoratum is an unsaturated lactone, which has many physiological properties.

(2) Coumarin is not present in sufficiently high quantities in A. odoratum to cause sweet clover disease in animals.

(3) Coumarin, normally a seed germination inhibitor, increases germination of A. odoratum seeds.

(4) Coumarin excreted by the roots of A. odoratum does not appear to affect the growth of associate plants but may have some effect on soil micro-organisms and hence on plants.

CHAPTER 9

DISEASES AND INSECT ATTACKS

9.1 INTRODUCTION

Although no study has been made in this thesis of the diseases affecting Anthoxanthum odoratum, it was felt that a brief literature review, some personal observations and the results from identifications of insects, kindly done by several workers, should be presented. Since A. odoratum is extremely adaptable and occurs in many diverse habits it could be assumed that it is a vigorous plant rarely attacked by diseases or insects, but it will be shown below that this is not the case.

9.2 FUNGI

They are found on all parts of the plant: leaves, stems, panicles and seed.

On the leaves and stems have been reported: Puccinia anthoxanthi Fuck. and Uredo anthoxanthina Bubak, which cause "browning" or "winter burn" (Stapledon and Davies, 1925). Sampson and Western (1954, p.15) state that the former is more destructive as it is a stem rust of the type P. graminis, forming long rusty-yellow sori on leaves and stems and in extreme cases seed production is lowered. McNabb (1962) is of the opinion that P. anthoxanthi is insufficiently distinct from P. graminis to treat it as a separate species; he prefers to call it P. graminis sens. lat.

U. anthoxanthina forms many short yellow-brown sori on the leaves; they lose colour and dry up in a bad attack. This species is also called Puccinia anthoxanthina (Bubak) Gäum., but McNabb (l.c.) considers it to be

identical with P. poae-nemoralis Otth. Fungal attacks were frequently observed in early summer on the single plants at Ilam in the experimental gardens of the Botany Department, University of Canterbury. On page 27, Sampson and Western (l.c.) report that Helminthosporium dematioideum Bubak and Wroblewski has been found on leaves of A. odoratum collected in Surrey, England.

Ergot, Claviceps purpurea (Fr.) Tul. has also been recorded on A. odoratum (Sampson and Western, l.c., p.32). White fungal growth has been observed at the panicle base of A. odoratum plants at Ilam. It is possible that this was an attack by choke, Epichloe typhina (Pers. ex Fr.) Ful., although this has not been verified.

On or in the seeds was found Aspergillus sp. (Mrs. M. Smith, pers. comm.) and Tilletia anthoxanthi Blytt. (Mr J.D. Allen, pers. comm.). The latter was first reported in New Zealand by Cunningham (1928). These fungi reduced germination (see Section 2.3).

On dead foliage, the saprophytic fungus Pithomyces chartarum (Berk. & Curt.) M.B. Ellis, which causes facial eczema in sheep, has been found, although in smaller quantities than observed on other pasture grasses (see Section 8.3.1). In that section, it has been shown that the lower facial eczema spore count is due to the presence of coumarin in the leaves of sweet vernal; it is well known that coumarin is an anti-fungal substance. It may seem surprising that so many different fungi have been reported on A. odoratum, but it could be that these fungi have developed races or species adapted to coumarin as the specific names of some of these fungi suggest.

9.3 VIRUSES

A.odoratum is a symptomless carrier of cereal yellow dwarf virus (Oswald and Houston, 1953), which may severely

infect Lolium perenne as Van den Bergh and Elberse (1962) found from their competition experiments between these two grasses (see Section 5.7.2). They suspect that A. odoratum may be host of other viruses as well.

Catherall (1966a) investigated the effect of cocksfoot streak virus (CSV) on Dactylis glomerata and and barley yellow dwarf virus (BYDV) on L. perenne. In conditions of interplant competition CSV was semi-lethal and BYDV was non-lethal. He found that CSV infection transformed plants of a pasture variety into "hay" types and BYDV infection transformed plants of a hay variety into "pasture" types. This affected the competitive ability of these types in sward conditions and demonstrated the significance of virus diseases for grassland productivity (see Section 5.7.2).

Catherall (1966b) also discovered a sap-transmitted mozaic virus in A. odoratum (most viruses are aphid-transmitted). It may thus be that A. odoratum is host of many other viruses which could affect the productivity of this species and other plants in its neighbourhood.

In Section 1.2, it has been suggested that variegated forms of A. odoratum, described by Domin (1941) as the forma pictum or picta, suffered from a virus disease. Variegation in a hexaploid wheat was found to be maternally inherited (Briggle, 1966) and it may be an example of cytoplasmic or non-chromosomal inheritance, since true breeding variegated lines could not be established. Dr H.C. Smith (pers. comm.) thinks that the photos of Briggle's variegated plants do not suggest that the plants had been affected by a virus, but in my opinion, it is still possible that a virus was transferred maternally. Briggle (l.c.) did not carry out a virus test on his plants. Virus-streaking in blades of A. odoratum was seen in the single plants at Ilam in the experimental grounds of the Botany Department,

and dwarfing expressed as reduction of culm length, assumed to be virus-induced was also observed (see Section 7.3). A study of the viruses affecting A. odoratum may yield interesting results because its wide distribution would make it, as hostplant, a potentially formidable source of infection to pasture grasses and cereals.

9.4 INSECT ATTACKS

Leaf miners were observed in young plants of A. odoratum. The insects were identified as Hydrellia tritici Coq. (Mr J.M. Kelsey, pers. comm.) and Cerodontha denticornis Panz. (Mr L.J. Dumbleton and Dr R.A. Harrison, pers. comm.). The latter informs me that C. denticornis is a very common leaf miner. Leaf miner damage can be considerable but rarely leads to the death of a plant since the growing point is not normally attacked.

Other insects which may do considerable damage to A. odoratum are thrips. They reduce the seed yield by destroying the grain as shown in Section 2.3 and in Table 2.9.a. Doull (1956, a, b, c) made a study of cocksfoot thrips which also occur in sweet vernal as will be shown below. His allegation that:"thrips have received little attention in New Zealand and the extent of the thrips of the country is not known....." (Doull, 1956 a), has been severely criticized by Spiller (1956) who presented a checklist of New Zealand Thysanoptera. I collected thrips from A. odoratum panicles in January 1964 at Ilam and forwarded them to Dr R. zur Strassen, Frankfurt am Main, who identified the following in the sample: about 40 specimens of Chirothrips manicatus, about 300 of Ch. (?) pallidicornis and about 30 of Aptinothrips rufus. He makes the following comments:

"The question mark in front of pallidicornis means that I am still not quite sure that it really is this species. The females from New Zealand cannot be distinguished from those in Europe or Central Asia but the males from New Zealand do not match those found in Central Asia (no males have been found so far in Europe)---. The species in the manicatus group belong to the most difficult complex in the genus Chirothrips." Although Doull's allegation may have been an exaggeration, it seems to me that the extent and distribution of the thrips found in New Zealand is insufficiently known.

Damage from grass grub, Costelytra zealandica Wh. has been observed in pot experiments. It reduced the greenness of the blades as if the plants suffered from a nutrient deficiency. On all subsequent experiments both in the glasshouse and in the field, DDT has been applied. It is remarkable that in spite of the very strong coumarin smell of A. odoratum roots, especially under dry conditions, grass grubs still eat these roots. Apparently coumarin does not affect the metabolism of the grubs.

No observations have been made on other insects.

9.5 SUMMARY

A. odoratum suffers from the following plant diseases and insect attacks:

(1) Fungi : Aspergillus sp.
Claviceps purpurea
Helminthosporium dematioideum
Pithomyces chartarum
Puccinia graminis
Puccinia poae-nemoralis
Tilletia anthoxanthi
(Epichloe typhina)

(2) Viruses : cereal yellow dwarf virus

a mozaic virus

(3) Insects : leaf miners:

Cerodontha denticornis

Hydrellia tritici

thrips:

Chirothrips manicatus

Chirothrips (?) pallidicornis

Aptinothrips rufus

grass grub:

Costelytra zealandica

CHAPTER 10

DISCUSSION AND CONCLUSION

10.1 INTRODUCTION

In this thesis evidence has been produced to support the claim that A. odoratum is a highly variable, highly adaptable colonizer with limited perenniality which persists in extremely diverse habitats. It has also been shown that groups of New Zealand plants of A. odoratum differ physiologically and morphologically, although they have been in this country for about one hundred years only. Whether these groups of plants represent definite or incipient ecotypes will now be discussed.

10.2 ECOTYPIC DIFFERENTIATION

Physiological differences among the A. odoratum plants from five localities studied in this thesis, have been demonstrated for the response to cold for floral induction (Section 2.6.3), for panicle emergence (Section 2.7.1), for various aspects of vegetative growth (Chapter 5, experiment A) and for nutrient uptake (Chapter 6); morphological differences have also been demonstrated (Chapter 7). Are these differences sufficient to permit recognition of these groups of plants as ecotypes?

10.2.1 Ecotype concept

The term "ecotype" has often been loosely used by botanists and agronomists. Ecotypic differentiation is a common phenomenon and although it may eventually give rise to the formation of ecotypes, it is usually incorrect to infer that ecotypes have already been formed. Heywood (see Davis and Heywood, 1963, p.402)

has made the following distinction to clarify misconceptions:

"(1) Environmental selection of genotypes most fitted to a particular habitat, and selective elimination of unfitted genotypes, giving a genetically adapted, heritable ecological product, the ECOTYPE.

(2) Environmental selection of genotypes which are able to grow in a range of habitats by consequence of their wide range of tolerance. The phenotypic product is termed an ECAD or MODIFICATION; ...".

Turesson coined the term ECOPHENE, but ECAD is more widely used.

It may seem to be unlikely that ecotypes have already developed in A. odoratum in New Zealand because selective elimination of unfitted genotypes does not occur rapidly in an outbreeder; it has many mechanisms to prevent this. It has been shown (Section 2.11) that sweet vernal seed may remain viable for a very long time; that the plant may stay alive for three to five years, possibly even longer under short sward conditions (Section 2.12) and Jones (1964) has shown that it has an extremely variable karyotype which slows down the elimination of a genotype which may be unfitted (Section 1.5). Therefore, it seems more correct to speak of ecads or modifications when discussing the groups of A. odoratum plants studied in this thesis.

On the other hand, Jain and Bradshaw (1966) and Ashton and Bradshaw (1966) have shown that in spite of the very considerable gene flow which is present in populations of outbreeders, differentiation does occur over very short distances, and that these morphological differences can be genetically fixed. These findings are of great importance because they are contrary to

the general statements made about outbreeders. For example, Davis and Heywood (l.c., p.380) stress that "outbreeders unlike inbreeders, tend to show a more or less continuous pattern of morphological variation. This tends to blur the distinction between populations; even when reproductive barriers exist, there is often a possibility of some gene-flow resulting in an overlapping morphological pattern".

In the case of the morphological differences among closely adjacent populations found by Bradshaw and his co-workers, one could speak of ecotypes although at first it looked as if they were dealing with ecads. The difference between ecotypes and ecads becomes clear-cut only after detailed experiments which demonstrate whether the characters investigated are genetically fixed or not.

Most of the experiments carried out in this thesis were done with seedlings grown from seed from the various sample sites. Only for the study of morphological differentiation (Chapter 7) were both seedlings and transplants used. However, that experiment did not show conclusively that the distinctness of the Lincoln plants was genetically fixed although it seemed likely that it was. The results from the physiological experiments showed winter-active behaviour and a lower vernalization requirement in the Kaikohe plants. These features gradually changed to a more winter-dormant behaviour and a higher vernalization requirement for the plants from further south until the montane Porter's Pass plants were shown to be decidedly winter-dormant. No such gradient was observed in the nutrient uptake experiment (Chapter 6), so that one can only speak of incipient ecotypy with respect to a certain character. Therefore, I prefer to follow Bradshaw by calling the groups of A. odoratum plants

studied here, part of a graded patchwork. If one wants to classify these incipient ecotypes, one may use the "Deme Terminology".

10.2.2 Deme concept

To keep micro-evolutionary units separate from orthodox taxonomical units, such as subspecies, varieties and forms, Gilmour and Gregor proposed in 1939 the "Deme Terminology", where the suffix "-deme", being "any group of individuals of a specified taxon", is enlarged by the addition of prefixes to describe the various units. The basic terms have been outlined by Davis and Heywood (l.c., p.411 f.f.) where it is also stressed that "no idea of population enters into the definition of the root, -deme". Throughout this thesis, I have tried to avoid the word "population" and have described the plants from various localities as "groups of plants". My groups of individual plants from the various sample sites could be called "physiotopodemes" since they are physiologically different groups from various localities, or "physioecodemes" if one wants to stress that the groups come from different kinds of habitats. The deme terminology has not been used in this thesis, because the physiological differences among the plants from the various localities varied with the character studied as stated in the previous section.

10.3 MICRO-EVOLUTION

Davis and Heywood report that several workers favour the idea that phenotypes (the outward appearance of a plant which alters in structure in response to changes in the environment) may ultimately achieve genetic fixity as a result of genetic pressures over a number of generations (Davis and Heywood, l.c. pp.405-6). Bradshaw and

his co-workers have shown that strongly selective environmental pressures can also bring about genetic fixity even in closely adjacent groups of plants and in spite of considerable gene flow. They stress that the stronger these selective pressures are, the sooner the genetic fixity becomes apparent and that certain characters respond more quickly to this pressure than other characters. Since the environmental pressures on the groups of A. odoratum plants studied here were not very great, it may explain that incipient ecotypy could be detected for certain characters only. The effect of strong environmental pressure was shown by the Porter's Pass plants. They were physiologically more distinct from the plants from the four lowland localities than the latter were among themselves so that altitude exerted a greater environmental pressure than latitude (see Chapter 5, experiment "A"). The absence of a well-defined pattern of response to the various characters measured in this thesis may thus be due to:

(1) the moderate environmental pressure to which most groups of A. odoratum plants were subjected,

(2) the difference in reaction of the various characters studied to environmental pressure.

However, it is clear that micro-evolution is taking place among these five groups of A. odoratum plants in New Zealand, just as it is in England in the Park Grass Plots at Rothamsted (Snaydon, 1963). As more investigations into ecotypic differentiation are being carried out, this phenomenon is becoming more apparent in different genera and species of plants and it is likely that this will be found to be common-place (Ashton and Bradshaw, 1966). For examples, see Durrant (1962) on Linum, Brougham and Harris (1967) on Lolium, and Baumeister (1967) on

several species.

How this micro-evolution is brought about has not been investigated. No ideograms of the chromosomes have been made. Chromosome counts of the morphologically distinct Lincoln plants showed that three out of four plants had 2n = 20 and the fourth 2n = 21 (Mr E.J.Beuzenberg, pers. comm.). It seemed as if the latter had an accessory chromosome which is common among Anthoxanthum species (Section 1.3); it was not one of the big plants.

Frankel (1954) has pointed out that the impact of a new environment on the genetic structure of introduced plants offers a very interesting research project for the evolutionary geneticist. It would therefore be worthwhile to use plants such as A. odoratum in New Zealand to find out whether mutations or simply recombinations of the existing genetic material can explain micro-evolution.

Recent investigations to explain the processes of adaptability and adaptation have been carried out by Grant (1963) and Wardlaw (1965). Although Grant (l.c.) stresses that adaptive changes to be inherited, must begin by being changes in the genic material of the reproductive cells, he also says that it is hypothetically possible, though not yet demonstrated, that the self-reproducing cytoplasmic determinants of some general process, like growth rate, might respond directly in concentration and intensity of action to external environmental conditions. Such responses, if carried out in the reproductive as well as the somatic cells, as might easily happen in plants with their production of flowers or cones on vegetative shoots, could conceivably be transmitted by inheritance. The second possibility to be considered (Grant, l.c.) is that the environmental influence affecting some organism might itself be the genetic material of another organism, in

which case, of course, it could produce a directed hereditary change in the former. Hereditary transformation is known to take place in the bacteria (for example in Pneumococcus). The processes of transformation and transduction in bacteria have no known counterparts in higher organisms. However, in my opinion, it is conceivable that viruses have a comparable effect on higher organisms as the work of Catherall suggests. He found that different viruses affect the growth form of grasses in different ways (see Section 9.3) and this transformation may possibly become hereditary.

Grant (l.c.) also points out that although the phenotypic reactions of organisms are not inherited, and hence do not lead directly to the evolution of new adaptive characteristics, the ability of an organism to adjust phenotypically to its environment does have evolutionary consequences. Phenotypic adjustments permit a group of plants to exist in an environment to which it is not well adapted and give it time to acquire, by a more or less random process of gene mutations, genotypes which are adapted to the new environment. This demonstrates that the evolutionary role of phenotypic reactions is indirect but not less real on that account.

Wardlaw (l.c.) discusses the existence of individuals in any group of plants which have different hereditary potentialities for adaptation to new or abnormal environmental conditions and stresses. These are the individuals which are likely to persist when natural selection operates and the potentialities of the next generation for acquiring the seemingly Lamarckian character will be increased. Wardlaw illustrates this acquiring of characters with Waddington's experiments with Drosophila raised on a salt medium. After 20 generations, a large number of salt-tolerant individuals

were present and even when the individuals were returned to their original environment, some of the "acquired" effects persisted. Waddington describes this phenomenon as "Genetic Assimilation", but he concludes that the acquired characters can only become hereditary by

(1) random mutations which are still the only known way in which new hereditary variation comes into existence,

(2) natural selection which is the only known process which is effective in changing the hereditary constitution of a population in successive generations.

It seems likely that plants under environmental stress are more receptive to random mutations than plants without stress. Waddington (see Wardlaw, l.c.) suggests that plants under stress may be set, as it were, on a hairtrigger and that once this state has been reached, it is relatively easy for other things besides the environment to pull the trigger. If genes are changing at random all the time, it will be by no means unlikely that a new mutation will turn up which suffices to pull the trigger and to fix genetically, the same acquired character which originally required an environmental stimulus to bring it into being.

From his work on adaptive changes in bacteria, Dean (see Wardlaw, l.c.) suggests that kinetic principles may be used to explain these changes. He considers that such principles explain the observed experimental results better than does a theory involving mutation and selection. Dean makes the following comments: "The question is often asked whether these adaptations represent stable heritable changes. It is our experience that in general the longer the training process has been continued, the more stable does

the adaptation become until eventually it appears to a cursory sort of test to be stable. But the stability is never absolute and so what we are dealing with are not stable heritable changes but sluggishly reversible adaptations. Kinetic theory in its simplest form predicts easy and complete reversibility on removal of the inducing agent, but there are good physico-chemical reasons why reversibility may on occasion be slow".

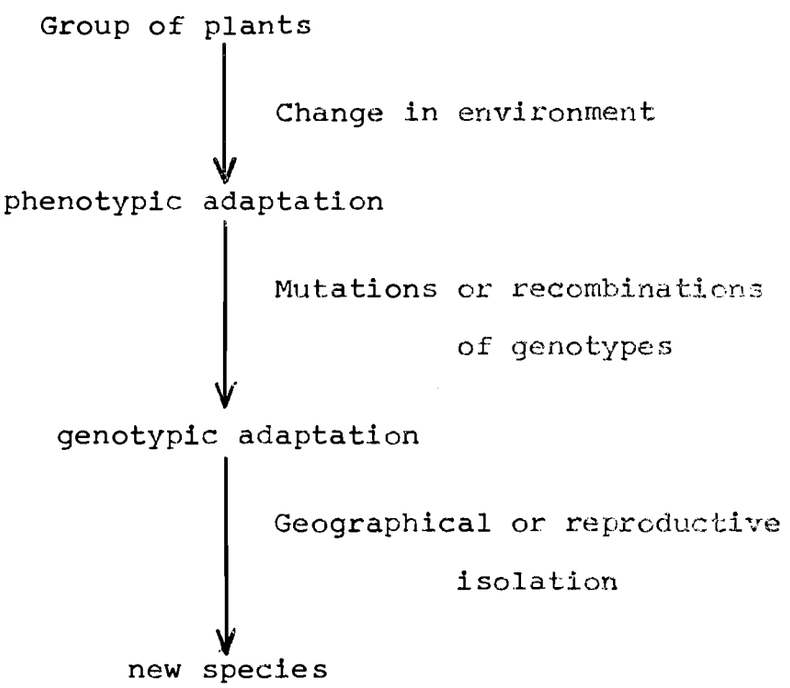
Dean's comments suggest that adaptations may seem to be heritable as if a mutation had occurred to fix the acquired character, but that it represents only one extreme of a sluggishly reversible physico-chemical process. In the same way, a plant breeder selects certain plants and by propagating and recombining only the superior plants, he may eventually obtain a new line of plants which appears to be genetically stable, although he has not consciously induced mutations to obtain this stability. However, he may have induced mutations unconsciously, because his plants were under stress and may have been subjected to the trigger mechanism suggested by Waddington above.

Whether mutations or physico-chemical processes determine adaptations is not clear. But it has been shown, not only in this thesis, but also by several other workers (see Wardlaw, l.c.) that adaptation in plants is much more related to physiological than to morphological features and it could thus be that the solution of the problem of micro-evolution may be in the hands of the biochemist - plant physiologist.

That micro-evolution can eventually lead to evolution of new species and genera has been demonstrated by the work of Beadle (1966). He has illustrated the importance of soil phosphate in moulding segments of the Australian flora. Taxa (mostly rainforest genera), adapted to high

phosphate levels have evolved new taxa with xeromorphic features suited to the low phosphate conditions prevalent in arid regions. These new taxa include very many new genera and some new species of genera that have persisted on soils of higher fertility. He suggests that this evolutionary process has been going on since early angiosperm times and that it is still operative today. Beadle emphasizes that soil phosphate must not be regarded as the only factor concerned in the evolution of the flora; other factors such as aridity, frost and salinity also play a role. However, in my opinion, he has shown that micro-evoltuion, primarily influenced by soil phosphate level, has given rise to new species and genera in Australia. Under suitable conditions, population differentiation giving rise to micro-evolution, may eventually lead to new species in other parts of the world also, although it may be less distinct because of less constancy in the environment.

From the results of the experiments described in this thesis and from the evidence from the literature produced in this section, the following diagram of micro-evolution has been drawn up:



Although micro-evolution usually progresses at a slow rate, it may be as important or even more so than the rapid and more obvious evolution caused by large environmental disturbances or by a mutation affecting the reproductive behaviour. Beadle's work illustrated that even a slow rate of evolution can lead to the formation of distinct species and genera. It will be a long time before this will happen to A. odoratum in New Zealand as long as it evolves at the present rate.

10.4 PLANT BREEDING POTENTIAL

Knowledge of incipient ecotypy and micro-evolution is of value to the plant breeder. It helps him to select among the wide range of material available those plants which will form the basis of a new strain or variety of species. One may say that the plant breeder speeds up the process of physiological adaptation and micro-evolution which appears to be going on all the time in nature. He steers this adaptation in the direction he desires, whether it be high productivity, improved nutritive value or any other factor required. In the initial stages of this breeding programme, the plant breeder will usually select from local material which is already well adapted for continued survival and production.

Since groups of A. odoratum plants in New Zealand are still highly variable in spite of incipient ecotypy, selection of desired plants could start among these groups if a plant breeding programme were to be initiated. There would be no need at this stage to introduce species and varieties from similar or slightly different climatic regions as has been done with considerable success in Britain, Australia (Breese, 1966; Cooper, 1965b) and New Zealand (Barclay, 1961). Because of its rather low

productivity (Section 4.4), early flowering (Section 2.7.2) and coumarin content (Chapter 8), it is unlikely that a plant breeding programme for A. odoratum will be started under the present economic conditions. However, it seems feasible to select A. odoratum plants which do not have the above disadvantages and still retain the advantage of survival under low soil fertility conditions. It could be argued that it may be cheaper to breed plants suited to a low fertility environment than to raise the fertility level of that environment so that the existing improved varieties of high fertility demanding species can survive there.

A. odoratum is easy plant breeding material because it is an outbreeder, but the appearance of stigmata and stamens before the culm has fully elongated is a slight drawback (see Section 2.7.2).

It has been shown in this thesis that the A. odoratum plants necessary for a breeding programme are available in New Zealand.

10.5 SUMMARY

(1) The groups of A. odoratum plants studied in this thesis show incipient ecotypy, but no ecotypes can be distinguished and no new taxa can be described.

(2) The distinctness of the degree of ecotypy varies with the character observed; physiological characters change sooner than morphological characters.

(3) Under the influence of different environmental pressures characters are modified at different stages and at different rates.

(4) Among the A. odoratum plants in New Zealand, sufficiently diverse material is available to start a breeding programme.

APPENDIX A

COLLECTION SITES

Since A. odoratum is a very polymorphic grass (Hubbard, 1954; Rozanova, 1925b; Strelkova, 1932), plants have been collected from various localities in New Zealand to obtain a general picture of some aspects of the biology of sweet vernal grass. Four localities, Kaikohe, Te Awa, Lincoln and Gore, are at or near substations of Grasslands Division, D.S.I.R., where new varieties of grasses and clovers are being tested. The fifth locality, a montane site at Porter's Pass, Canterbury, was especially chosen on account of the importance of A. odoratum in the South Island high country. The sites were either undisturbed road sides or very infrequently grazed permanent pastures, so that it was assumed that the plants had become adapted to their respective sites and that the sites were comparable.

Most collection sites measured about 100 m^2.

1. KAIKOHE COLLECTION SITE

At Grasslands Division, D.S.I.R., Substation, Kaikohe; from a short grass pasture opposite the office block near the climate plot. The flat area was grazed infrequently.

Reference NZMS 1:N 15: 327334, alt. 183 m.

Coordinates approx.: 35° 25' S, 173° 49' E.

Soil type: Wharekohe silt loam.

The botanical composition of this pasture on 19-4-'63 is shown in Table A.a.

2. TE AWA COLLECTION SITE

At Te Awa Hill Pasture Research Area, Grasslands Division, D.S.I.R.; from a 3 sheep/acre block which was the control block, three years before the collection was made. The plants were from an area close to a macrocarpa shelter belt near the track on the main ridge. The area had a SSW aspect, slope approx. 20°.

Reference NZMS 1:N 144: 265617, alt. 320 m.

Coordinates approx.: 40° 08' S, 175° 47' E.

Soil type: Pohangina sandy loam.

The botanical composition of this pasture on 17-4-'63 is shown in Table A.a.

3. LINCOLN COLLECTION SITE

At junction of Prebbleton-Ladbrooks Road and Trices Road near Prebbleton in a strip adjoining the railway line. This flat area was completely untouched. The railway line is an infrequently used branch line and a fire from hot ashes must be exceptionally rare.

Reference NZMS 1:S 83: 892490, alt. 20 m.

Coordinates approx.: 43° 35' S, 172° 31' E.

Soil type: Eyre-Paparua recent soil.

The botanical composition of this area on 9-5-'63 is shown in Table A.a.

4. GORE COLLECTION SITE

Along a shingle road near a fence, north of Greenvale. The flat site may be grazed or mown occasionally.

Reference NZMS 1:S 161: 919702, alt. 243 m.

Coordinates approx.: 45° 52' S, 169° 03' E.

Soil type: Waikoikoi yellow-grey to yellow-brown earth intergrade.

The botanical composition of this area on 14-4-'63 is shown in Table A.a.

5. PORTER'S PASS COLLECTION SITE

At the top of the Pass, to the north of the road on a nearly flat area of disturbed tall tussock grassland. The area had a SSE aspect, slope approx. 4°.

Reference NZMS 1:S 74: 214854, alt. 945 m.

Coordinates approx.: 43° 18' S, 171° 45' E.

Soil type: Kaikoura steepland yellow-brown earth.

The vegetation consisted of Chionochloa rigida, Festuca novae-zelandiae, Poa colensoi, Agrostis tenuis, Agropyron scabrum, Notodanthonia gracilis, Deyeuxia avenoides, Dracophyllum uniflorum, Cassinia fulvida, Viola cunninghamii, Cyathodes fraseri, Raoulia subsericea, Lycopodium fastigiatum, Luzula sp., Senecio bellidioides, Hypochaeris radicata, Pimelea oreophila, Wahlenbergia albomarginata, Rumex acetosella, Epilobium elegans, Gaultheria depressa, Scleranthus uniflorus and Helichrysum filicaule.

6. DRY CREEK COLLECTION SITE

A few miles beyond Porter's Pass (towards Castle Hill basin) on a more exposed site and at a higher altitude. The site was a badly disturbed tall tussock grassland community and much shingle was showing; plant cover up to 20%. The area had a NNE aspect, slope approx. 20°.

Reference NZMS 1:S 74: 195893, alt. 1035 m.

Coordinates approx.: 43° 16' S, 171° 43' E.

Soil type: Tekoa steepland yellow-brown earth.

The sparse vegetation consisted of Chionochloa rigida, Poa colensoi, Rumex acetosella, Hypochaeris radicata, Wahlenbergia albomarginata, Raoulia subsericea and one plant of Holcus lanatus.

TABLE A.a Botanical composition of collection sites

COLLECTION SITE	KAIKOHE		TE AWA			LINCOLN			GORE
SAMPLING DATE	19-4-1963		17-4-1963			9-5-1963			14-4-1963
SAMPLING METHOD*	A		A		B	A		B	B
	Tillers	Freq.	Tillers	Freq.	Wt. %-age	Tillers	Freq.	Wt. %-age	Wt. %-age
Anthoxanthum odoratum	112	23	62	28	7.6	449	73	48.1	16.4
Agrostis tenuis	1067	98	657	93	68.7				58.2
Festuca rubra			69	20	12.1	19	10		1.0
Dactylis glomerata	6	3	4	4	5.8	5	4	3.4	8.4
Poa pratensis			15	6				4.1	1.6
Holcus lanatus	11	8	26	18	5.8				9.8
Agropyron scabrum			20	7		68	26	13.8	
Cynosurus cristatus	101	20	17	8					
Notodanthonia racemosa						169	47	23.6	
Paspalum distichum	46	9							
Trifolium repens	30	19	14	6	Trace				1.4
Trifolium pratense									Trace
Trifolium campestre						1	1		
Lotus pedunculatus	144	47	4	1					
Vicia sp.						33	26	5.1	Trace
Hypochaeris radicata	34	23	1	1					
Ranunculus acer	5	3	1	1					
Prunella vulgaris	1	1							
Luzula sp.			1	1					
Juncus gregiflorus	7	3							
Plantago lanceolata	29	17				2	2	1.9	
Crepis capillaris	12	9							
Mentha pulegium	13	1							
Leontodon autumnalis									Trace
Chrysanthemum leucanthemum									Trace
Cirsium arvense									Trace
Achillea millefolium									3.2

*METHOD A : Determined from 100 tiller-plugs (each plug 5 cm in diameter)
METHOD B : Determined from percentages by weight

7. LOWER CRAIGIEBURN RANGE EXPERIMENTAL SITE

On bare exposed sub soil in fenced area beyond solitary mountain beech trees, about 150 m. along the Canterbury Winter Sports Club ski road below "Middle Hut". The fence excluded sheep but not deer, rabbits, hares, grasshoppers and other grazing animals. The area had a NE aspect, slope about 22°.

Reference NZMS 1: S 66: 161022, alt. 1220 m.

Coordinates approx.: 43° 09' S, 171° 40' E.

Soil type: Bealey steepland yellow-brown earth

The site itself was bare with moving shingle and soil but in the locality was found: Dracophyllum uniflorum, Cyathodes fraseri, C. colensoi, Chionochloa rigida, Poa colensoi, Celmisia spectabilis, Rumex acetosella and Epilobium sp.

8. UPPER CRAIGIEBURN RANGE EXPERIMENTAL SITE

In alpine tussock grassland above "Tophut" of the Canterbury Winter Sports Club on left hand side of track to ski basin. The plants were under cages which excluded all grazing animals except grasshoppers, field mice and similar small animals. The area had an ENE aspect, slope about 16°.

Reference: NZMS 1:S 66: 148022, alt. 1585 m.

Coordinates approx.: 43° 09' S, 171° 39' E.

Soil type: Kaikoura steepland yellow-brown earth.

The site had about 50% bare ground, mostly rock. The vegetation consisted of Chionochloa rigida, Ch. pallens, Celmisia lyallii, C. viscosa, Anisotome flexuosa, Poa colensoi, Raoulia subsericea, R. bryoides, Blechnum penna-marinum, Lycopodium fastigiatum, Hymenanthera alpina, Carex sp., Luzula sp., Uncinia sp. and Wahlenbergia albomarginata.

LITERATURE

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